Environment Canada Environnement Canada

Anthony J. Gaston
Todd E. Golumbia
Jean-Louis Martin
Sean T. Sharpe
(editors)

Lessons from the Islands

Introduced species and what they tell us about how ecosystems work

Special Publication
Canadian Wildlife Service

Canada

Anthony J. Gaston
Todd E. Golumbia
Jean-Louis Martin
Sean T. Sharpe
(editors)

Lessons from the Islands
Introduced species and what they tell us about how ecosystems work

Special Publication
Canadian Wildlife Service

Proceedings from the Research Group on Introduced Species 2002 Symposium held in Queen Charlotte City, British Columbia, on 1–5 October 2002

Également disponible en français sous le titre
Leçons des îles : Les espèces introduites et ce qu'elles nous apprennent sur le fonctionnement des écosystèmes.
Environnement Canada, publication spéciale

This document may be cited as follows:

Gaston, A.J.; Golumbia, T.E.; Martin, J.-L.; Sharpe, S.T. (eds). 2008. Lessons from the Islands: introduced species and what they tell us about how ecosystems work. Proceedings from the Research Group on Introduced Species 2002 Symposium, Queen Charlotte City, Queen Charlotte Islands, British Columbia. Canadian Wildlife Service, Environment Canada, Ottawa

Cover
Background photo
Caption: Fog and shoreline at SGang Gwaay
Credit: RGIS, Jean-Louis Martin
Photo of swimming deer
Credit: RGIS, Tony Gaston

Inside of front cover:
Caption: Satellite image of Haida Gwaii
Credit: Gowgaia Institute, Box 638, Queen Charlotte, Haida Gwaii, Canada V0T 1S0, www.spruceroots.org

Inside of back cover:
Caption: Satellite image of Laskeek Bay
Credit: Gowgaia Institute, Box 638, Queen Charlotte, Haida Gwaii, Canada V0T 1S0, www.spruceroots.org

© Her Majesty the Queen in Right of Canada, represented by the Minister of Environment, 2008. All rights reserved.

Catalogue no. CW69-20/1-2007E
ISBN 978-0-662-45995-8

On line in HTML and PDF at http://www.cws-scf.ec.gc.ca/publications
Catalogue no. CW69-20/1-2007E-PDF
ISBN 978-0-662-45996-5

Library and Archives Canada Cataloguing in Publication

Lessons from the islands : introduced species and what they tell us about how ecosystems work / Anthony J. Gaston ...[et al.] (editors).

(Special publication / Canadian Wildlife Service)
"Proceedings from the Research Group on Introduced Species 2002 Symposium held in Queen Charlotte City, British Columbia, on 1-5 October 2002".
Issued also in French under title: Leçons des îles, les espèces introduites et ce qu'elles nous apprennent sur le fonctionnement des écosystèmes.
Includes bibliographical references.
Available also on the Internet.
ISBN 978-0-662-45995-8
Cat. no.: CW69-20/1-2007E

1. Mule deer--Ecology--British Columbia--Queen Charlotte Islands --Congresses. 2. Biotic communities--British Columbia--Queen Charlotte Islands --Congresses. 3. Animal introduction--British Columbia--Queen Charlotte Islands--Congresses. 4. Forest ecology--British Columbia--Queen Charlotte Islands --Congresses. 5. Wildlife management--British Columbia--Queen Charlotte Islands --Congresses. 6. Ecology--British Columbia--Queen Charlotte Islands--Congresses. 7. Restoration ecology--British Columbia--Queen Charlotte Islands--Congresses. 8. Deer--Ecology--North America--Congresses. 9. Animal introduction--North America--Congresses. I. Gaston, A. J. II. Canadian Wildlife Service III. Title.

IV. Series: Special publication (Canadian Wildlife Service).

QL737.U55 2007 333.95'96530971112 C2007-980119-6

March 2008

About the Research Group on Introduced Species and the 2002 Symposium

The Research Group on Introduced Species (RGIS) was founded in 1996 to conduct research and publicize information on the effects of introduced species on natural ecosystems within the Haida Gwaii (Queen Charlotte Islands) archipelago in British Columbia, Canada. In 2001, it was registered as a nonprofit trust based in Queen Charlotte City. It works in collaboration with several federal and provincial government agencies (Environment Canada, Parks Canada Agency, and the B.C. Ministry of Environment), with the Centre national de la recherche scientifique, Montpellier, France, and with a local conservation group, the Laskeek Bay Conservation Society.

The main thrust of RGIS projects has been to explore the impacts of introduced black-tailed deer and, to a lesser extent, red squirrels on forest ecology in the archipelago. The emphasis has been on natural forest ecosystems, but work on commercially managed forests has also been conducted. A major field program, aimed at elucidating the costs of the deer introduction to the overall biodiversity of the archipelago, was conducted during 1996–2002, involving 14 scientists and 9 graduate students.

Part of the mandate of the RGIS is to improve the dissemination of information about introduced species and the consequences of overabundant ungulate populations, both on Haida Gwaii and farther afield. To this end, a symposium was convened in Queen Charlotte City in October 2002 to review the results of RGIS projects to that date, to obtain reactions from local people, and to promote future activity towards introduced species control in the Queen Charlotte Islands. In addition, the RGIS invited the participation of several senior researchers with experience in introduced species or ungulate overabundance problems throughout North America, especially those involving deer. Their presence was important in bringing a broader perspective to the meeting and in making available experience obtained elsewhere.

This volume comprises the following sections:

- *Background*—an introduction to the ecology of Haida Gwaii and of the black-tailed deer in the forests of the Pacific rim and a description of the history of vertebrate introductions in the archipelago;
- *Lessons from the Islands*—reviews of research on biodiversity impacts of introduced deer and squirrels carried out by the RGIS;
- *Restoration: potential and challenges*—descriptions of the deer culls carried out on two islands, the resulting vegetation recovery, and the likelihood of deer reimmigration;
- *Lessons from elsewhere*—a review of introduced species impacts and case studies of deer introductions, deer overabundance, and deer management elsewhere in North America; and
- *Conclusions*—brief summaries of the symposium outputs.

Acknowledgements

Funding for the research of the Research Group on Introduced Species was provided by Environment Canada; Parks Canada Agency (Gwaii Haanas National Park Reserve and Haida Heritage Site); the Canada–British Columbia South Moresby Forest Replacement Account (SMFRA) (Contract No. SMFRA99DQC-002, SMFRA Project 24.2, "Pattern of Western Red Cedar Regeneration"); the Centre National de la Recherche Scientifique and the Ministry of Foreign Affairs of France (PICS 489); and Forest Renewal British Columbia, a partnership of forest companies, workers, environmental groups, First Nations, communities, and the government of British Columbia (Research Award PA97335-BRE) (Forest Renewal BC funding—from stumpage fees and royalties that forest companies pay for the right to harvest timber on Crown lands—is reinvested in forests, forest workers, and forest communities). Funding assistance by Forest Renewal BC does not imply endorsement of any statements or information contained herein. Environment Canada, Parks Canada Agency, and the Laskeek Bay Conservation Society provided valuable logistic support. The British Columbia Ministry of Environment, Skeena Region, gave permission to conduct research in the Wildlife Management Area of Laskeek Bay, and the Archipelago Management Board gave permission for research conducted in Gwaii Haanas National Park Reserve.

We thank all those who worked with us during 1996–2002 in the field, in the laboratory, and in the library, and all the colleagues who provided expertise and assistance in the disciplines with which we were less familiar. Special thanks go to our students: Sylvain Allombert, Christophe Baltzinger, Isabel Buttler, Tanguy Daufresne, Christian Engelstoft, Mathieu Joron, Steve Stockton, Bruno Vila, and Gwenaël Vourc'h; and to our coordinators: Barb Rowsell, Greg Martin, and Tarmo Poldmaa. We thank Kathy Martin for a complete review of the final document. Particular thanks for a whole range of services go to Rob Kelly. We are most grateful to the people of Haida Gwaii for their help and patience during the carrying out of this research. The work of individuals in association with the various RGIS projects is acknowledged in the relevant papers.

This publication was produced by Publishing and Creative Services in the Communications Branch of Environment Canada. The following people were responsible: Maureen Kavanagh, Susan Burns, and Pierre Faucher—coordination; Linda Bartlett and Georgiana Chung—layout; Marla Sheffer (contract editor)—scientific editing; France D. Bélanger—French editing and Chris Pitre—English proofreading and Nicole Parent—French proofreading.

Contents

Contributors	vi
Frontispiece A	viii
Frontispiece B	ix
Background	
An introduction to the plant ecology of Haida Gwaii Jim Pojar	3
History and current status of introduced vertebrates on Haida Gwaii Todd Golumbia, Lisa Bland, Keith Moore, and Patrick Bartier	8
Changes in vegetation of Haida Gwaii in historical time Jim Pojar	32
Ecology of black-tailed deer in north coastal environments Michael P. Gillingham	39
A conceptual framework for introduced species research in Haida Gwaii Anthony J. Gaston and Jean-Louis Martin	48
Lessons from the Islands	
Introduction to the terrestrial ecology of Laskeek Bay Stephen A. Stockton and Anthony J. Gaston	55
Spread and history of deer impact: the memory of the woody plants Bruno Vila and Jean-Louis Martin	57
The effects of deer on plant diversity Stephen A. Stockton	64
Interaction between Sitka black-tailed deer and western redcedar: lessons from Haida Gwaii Gwenaël Vourc'h, José Escarré, and Jean-Louis Martin	70
Herbivory and the missing understory on Haida Gwaii Christian Engelstoft, Matthew D. Kirchhoff, and Donald Eastman	78
The effects of deer on invertebrate abundance and diversity Sylvain Allombert and Jean-Louis Martin	87
The effects of deer and squirrels on forest birds: community structure, population density, and reproduction Jean-Louis Martin, Sylvain Allombert, and Anthony J. Gaston	93
Restoration: Potential and challenges	
Reduction in deer numbers on Reef Island and SGang Gwaay: progress, results, and vegetation changes Anthony J. Gaston, Sean Sharpe, Stephen A. Stockton, Todd Golumbia, and Jean-Louis Martin	103
Estimating deer colonization rates to offshore islands of Haida Gwaii using microsatellite markers Tom E. Reimchen, R.J. Nelson, and C.T. Smith	117
Lessons from elsewhere	
Science and the management of introduced species Daniel Simberloff	123
White-tailed deer impacts in North American and the challenge of managing a hyperabundant herbivore Donald M. Waller	135
White-tailed deer population reduction and control in four southwest Ontario protected heritage areas Dan Reive and Bill Stephenson	148
High herbivore density and boreal forest ecology: white-tailed deer on Anticosti Island Steeve D. Côté, Christian Dussault, Jean Huot, François Potvin, Jean-Pierre Tremblay, and Vanessa Viera	154
Social and natural history of moose introduced to Newfoundland Brian E. McLaren	162
The Alaska perspective—deer populations in the presence of wolves Matthew D. Kirchhoff and David K. Person	171
Conclusions	
Deer and biodiversity on Haida Gwaii: lessons, questions, and decisions Jean-Louis Martin, Anthony J. Gaston, Todd Golumbia, and Sean Sharpe	183
A conceptual framework for introduced species management in Haida Gwaii Todd Golumbia and Barb Rowsell	186

Contributors

Sylvain Allombert
Centre national de la recherche scientifique, CEFE-UMR5175, 1919 route de Mende, F-34293 Montpellier Cedex 5, France

Patrick Bartier
Gwaii Haanas National Park Reserve and Haida Heritage Site, Box 37, Queen Charlotte City, BC, Canada V0T 1S0

Lisa Bland
Consultant, Queen Charlotte City, BC, Canada V0T 1S0

Steeve D. Côté
Chaire de recherche industrielle CRSNG–Produits forestiers Anticosti, Département de biologie et Centre d'études nordiques, Université Laval, Québec, QC, Canada G1K 7P4

Christian Dussault
Chaire de recherche industrielle CRSNG–Produits forestiers Anticosti, Département de biologie et Centre d'études nordiques, Université Laval, Québec, QC, Canada G1K 7P4

Donald Eastman
Department of Biology, University of Victoria, P.O. Box 3020, Station CSC, Victoria, BC, Canada V8W 3N5

Christian Engelstoft
Department of Biology, University of Victoria, P.O. Box 3020, Station CSC, Victoria, BC, Canada V8W 3N5

José Escarré
Centre national de la recherche scientifique, CEFE-UMR5175, 1919 route de Mende, F-34293 Montpellier Cedex 5, France

Anthony J. Gaston
Canadian Wildlife Service, National Wildlife Research Centre, 1125 Colonel By Drive (Raven Road), Ottawa, ON, Canada K1A 0H3

Michael P. Gillingham
Natural Resources and Environmental Studies, University of Northern British Columbia, 3333 University Way, Prince George, BC, Canada V2N 4Z9

Todd Golumbia
Gwaii Haanas National Park Reserve and Haida Heritage Site, Box 37, Queen Charlotte City, BC, Canada V0T 1S0 (present address: Gulf Islands National Park Reserve, 2220 Harbour Road, Sidney, BC, Canada V8L 2P6)

Jean Huot
Chaire de recherche industrielle CRSNG–Produits forestiers Anticosti, Département de biologie et Centre d'études nordiques, Université Laval, Québec, QC, Canada G1K 7P4

Matthew D. Kirchhoff
Alaska Department of Fish and Game, P.O. Box 240020, Douglas, AK 99824, USA

Jean-Louis Martin
Centre national de la recherche scientifique, CEFE-UMR5175, 1919 route de Mende, F-34293 Montpellier Cedex 5, France

Brian E. McLaren
Newfoundland and Labrador Department of Forest Resources and Agrifoods, P.O. Box 2222, Gander, NL, Canada A1V 2N9 (present address: Faculty of Forestry and Forest Science, Lakehead University, Thunder Bay, ON P7B 5E1)

Keith Moore
Moore Resource Management, Queen Charlotte City, BC, Canada V0T 1S0

R.J. Nelson
British Columbia Forest Service, Postal Bag 5000, Smithers, BC, Canada V0J 2N0

David K. Person
Division of Wildlife Conservation, Alaska Department of Fish and Game, 2030 Sea Level Drive, Ketcikan, AK 99907, USA

Jim Pojar
British Columbia Forest Service, Postal Bag 5000, Smithers, BC, Canada V0J 2N0

François Potvin
Société de la Faune et des Parcs du Québec, Direction de la recherche sur la faune, 675 boul. René-Lévesque est, Québec, QC, Canada G1R 5V7

Tom E. Reimchen
Department of Biology, University of Victoria, Victoria, BC, Canada V8W 3N5

Dan Reive
Point Pelee National Park, 407 Monarch Lane, RR #1, Leamington, ON, Canada N8H 3V7

Barb Rowsell
Research Group on Introduced Species, Box 847, Queen Charlotte City, BC, Canada V0T 1S0

Sean Sharpe
British Columbia Ministry of Environment, Lands and Parks (now Ministry of Environment), P.O. Bag 5000, Smithers, BC, Canada V0J 2N0

Daniel Simberloff
Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996-1610, USA

C.T. Smith
Department of Biology, University of Victoria, Victoria, BC, Canada V8W 3N5

Bill Stephenson
Parks Canada Agency, Ecosystem Conservation Section, 111 Water Street East, Cornwall, ON, Canada K6H 6S3

Stephen A. Stockton
Department of Biology, University of Ottawa, Ottawa, ON, Canada K1N 6N5
(present address: 27 Bannockburn Ave., Toronto, ON M5M 2M7)

Jean-Pierre Tremblay
Chaire de recherche industrielle CRSNG–Produits forestiers Anticosti, Département de biologie et Centre d'études nordiques, Université Laval, Québec, QC, Canada G1K 7P4

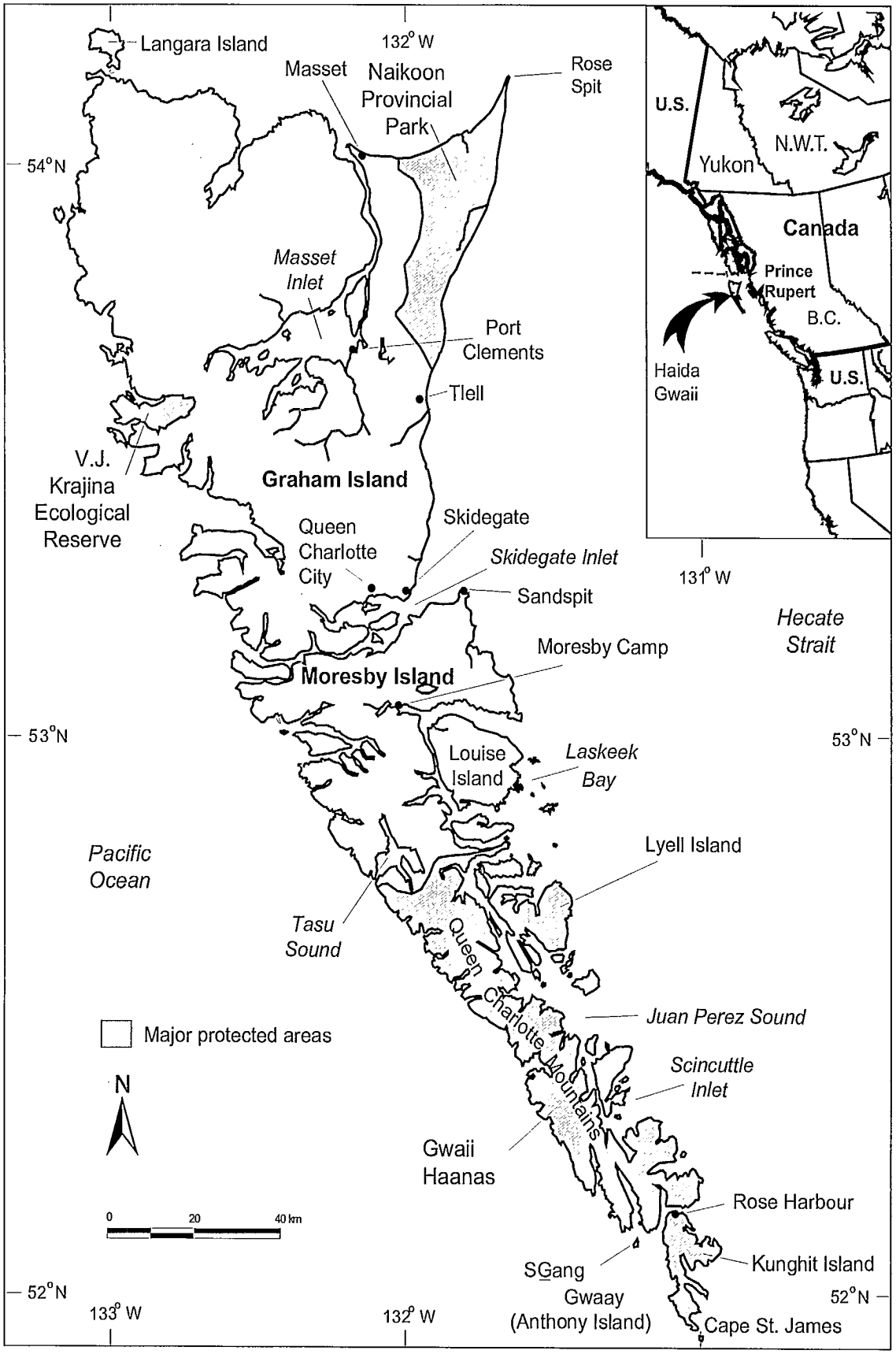
Vanessa Viera
Chaire de recherche industrielle CRSNG–Produits forestiers Anticosti, Département de biologie et Centre d'études nordiques, Université Laval, Québec, QC, Canada G1K 7P4

Bruno Vila
Institut Méditerranéen d'Écologie et de Paléoécologie / Centre National de la Recherche Scientifique, UMR6116, Faculté des sciences et techniques de Saint-Jérôme, Avenue Escadrille Normandie Niemen, F-13397 Marseille Cedex 20, France

Gwenaël Vourc'h
Unité d'Épidémiologie Animale, Institut National de la Recherche Agronomique, 63122 Saint-Genès-Champanelle, France

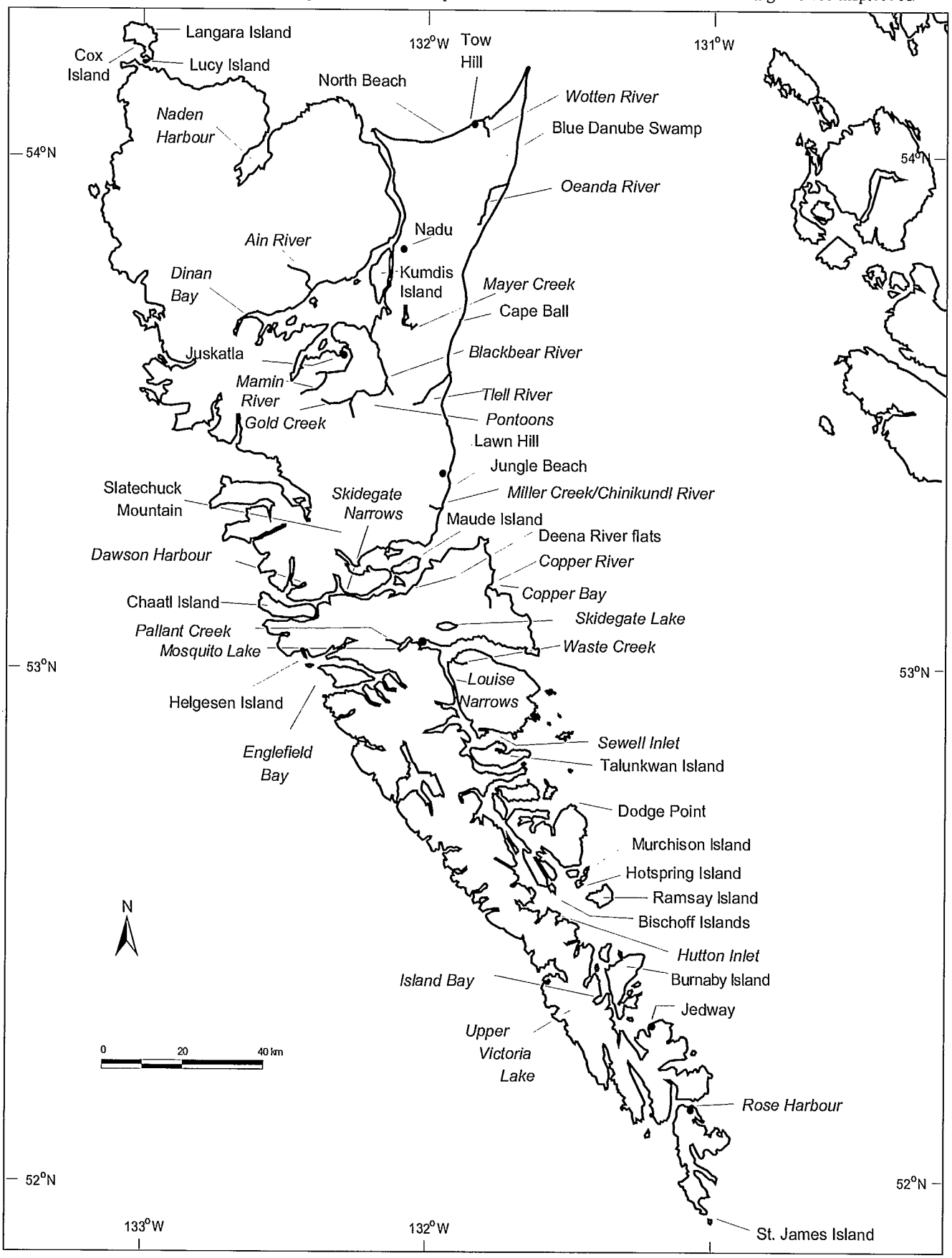
Donald M. Waller
Department of Botany & Environmental Studies, University of Wisconsin – Madison, Madison, WI 53706, USA

Frontispiece A
Haida Gwaii, which means "Islands of the people" in the Haida language, is better known as the Queen Charlotte Islands. For additional place names, see Frontispiece B on facing page and maps of Laskeek Bay (pages 55 and 62) and SGang Gwaay (page 105).



Frontispiece B

This map complements Frontispiece A and provides additional place names that would not fit without crowding into Frontispiece A.



Background

Caption: A view of De la Bêche Inlet
Credit: RGIS, Jean-Louis Martin

An introduction to the plant ecology of Haida Gwaii

Jim Pojar

1. Physical setting

1.1 Location and size

Haida Gwaii is the most remote island archipelago in Canada and consists of over 350 islands 50–130 km off the northern mainland coast of British Columbia (Fig. 1). The two main islands, Graham and Moresby, together constitute nine-tenths of the total 995 000-ha area of the group.

1.2 Protected areas on Haida Gwaii

Haida Gwaii includes three large, formally protected areas. Naikoon Park (71 000 ha) was created in 1973 to preserve 100 km of beaches and dunes, along with sphagnum bogs and coastal temperate rainforest. Gwaii Haanas (147 000 ha), which constitutes approximately 15% of Haida Gwaii and encompasses over 200 islands, was established in 1988 to protect marine, intertidal, and terrestrial ecosystems as well as a diverse and rich cultural history. The V.J. Krajina Ecological Reserve (7800 ha) on the west coast of Graham Island contains productive temperate rainforest as well as rare species of vascular plants and bryophytes (B.C. Parks 1992). These areas protect a significant land base (23% of the archipelago), representing a broad spectrum of island species and ecosystems. There are several other ecological reserves, small but biologically very significant, including Rose Spit, Tow Hill Bog, Drizzle Lake, and Lepas Bay.

1.3 Physiography and bedrock geology

There are three physiographic regions on the archipelago (Brown 1968): 1) the Queen Charlotte Ranges, forming the rugged, mountainous western region; 2) the Skidegate Plateau, a partially dissected peneplain of the north-central region; and 3) the Queen Charlotte Lowland—plains and low hills of the northeastern region.

Haida Gwaii has a complex bedrock geology, with hard and soft volcanic, sedimentary, and acid intrusive rocks well represented (Brown 1968; Brown and Yorath 1989). The productive forests of the Skidegate Plateau and Queen Charlotte Ranges are underlain mainly by volcanic rocks, with some minor but very productive sedimentary rocks. Sedimentary rocks underlie most of the deep surface deposits (glacial and marine) on the Queen Charlotte Lowland. Intrusive bedrock is largely restricted to the Queen Charlotte Ranges, where it and the hard volcanics tend to support low-productivity forest and sloping bogs.

1.4 Climate

The climate is a cool temperate, oceanic, humid–perhumid type. Late fall and early winter are very wet. Winter is cool but mild, rainy, and snowy. Snowpack along the coast is usually ephemeral, but more snow falls at higher elevations (especially above 600 m) and in the interior of the larger islands. Summer is cool and wet, but sometimes has dry warm spells. Cloud cover is very common, and fog is frequent. Strong winds are common and form an important climatic feature. Mean annual temperature of the tidewater stations is 8°C; daily, seasonal, and annual ranges in air temperature are narrow. Recorded mean annual precipitation ranges from 1100 to 4200 mm (Environment Canada 1980). The Queen Charlotte Ranges cast a rain shadow on eastern Graham and Moresby islands, resulting in a decrease in annual precipitation from an estimated 5000+ mm on some of the windward slopes to around 1000 mm on the eastern lowlands (G.O.V. Williams in Calder and Taylor 1968).

2. Present-day vegetation

2.1 Temperate rainforest biome

The plant cover of Haida Gwaii is a complex of forests and nonforested wetland, maritime, and high-elevation communities (Banner et al. 1983, 1989; Pojar and Broadhead 1984). There is a full range of ecosystems and successional stages. Nevertheless, the landscape is largely forested, and, over most of preindustrial time, most of the forests were old. As a consequence of a history of infrequent, large-scale, stand-destroying disturbances in a wet, mild, mountainous environment, productive forests are characterized by big old trees, tremendous accumulations of biomass, coarse woody debris (downed logs plus standing dead trees, or snags) as a key structural component, and gap dynamics (i.e., most tree replacement occurs on a tree-by-tree basis, with regeneration in gaps resulting from the death of individual or small groups of canopy trees) (Pojar and

MacKinnon 1994; Lertzman et al. 1997).

Coastal temperate rainforest is a globally rare biome, represented in North America by the dense evergreen Pacific Coast Conifer Forest, which stretches from northern California through southeast Alaska (Barbour and Billings 1988). Over the past century, this biome has been reduced to only 44% of an estimated original extent of 25 million hectares, with most of the remaining forest occurring north of 48°N (Schoonmaker et al. 1997). Haida Gwaii, with over 540 000 ha of intact temperate rainforest, contains a significant portion of what remains (Alaback and Pojar 1997). Western hemlock Tsuga heterophylla,1 western redcedar Thuja plicata, and Sitka spruce Picea sitchensis dominate the closed coniferous forest of Haida Gwaii at low elevations, while mountain hemlock Tsuga mertensiana and yellow-cedar or cypress Chamaecyparis nootkatensis gain in importance at higher elevations. Yellow-cedar and shore pine Pinus contorta var. contorta join western (and often mountain) hemlock, western redcedar, and Sitka spruce in boggy windward forests.

2.2 Zonal forests

Mature and old stands on zonal (average) sites at low to moderate elevations typically have abundant natural regeneration of western hemlock. Usually there is little if any regeneration of either western redcedar or yellow-cedar and scattered spruce regeneration in openings. The overstory trees form a dense canopy that casts deep shade, although old-growth forests have ragged canopies with frequent gaps that allow patchy penetration of light. Bryophytes carpet the forest floor, and epiphytic mosses and lichens are also abundant. However, there is a conspicuous lack of understory shrubs (except for hemlock regeneration) and herbs. The sparse understory appears to be a function of shade (shrubs and herbs that do occur are most frequent in forest gaps) and browsing by deer. Typical scattered shrubs are species of Vaccinium (red huckleberry V. parvifolium, Alaska blueberry V. alaskaense, oval-leaved blueberry V. ovalifolium), false azalea Menziesia ferruginea, salal Gaultheria shallon, and western yew Taxus brevifolia. Characteristic herbs include ferns (deer fern Blechnum spicant, spiny wood fern Dryopteris assimilis), twayblade orchids Listera caurina and L. cordata, twisted-stalks Streptopus amplexifolius and S. lanceolatus, bunchberry Cornus canadensis, spleenwort-leaved goldthread Coptis asplenifolia, and single delight Moneses uniflora.

2.3 Azonal forests[1]

Dry forests are uncommon and dominated by western redcedar, western hemlock, and occasionally shore pine, often with a fair amount of salal in the understory. Moist but freely drained sites on slopes support vigorous mixtures of western hemlock and Sitka spruce, with a component of yellow-cedar at higher elevations. The most impressive forests on the islands occur on recent alluvial deposits adjacent to streams and on fluvial/colluvial fans in gullied terrain. Large, tall, widely spaced spruce and hemlock dominate such stands, the shrub layer is sparse, and the ground cover is often grassy rather than ferny and mossy. Sitka spruce forests also have developed along marine shorelines, on stabilized sand dunes, and on rocky headlands and steep slopes exposed to salt spray.

Wet, rather scrubby forests are common on subdued, poorly drained terrain generally, especially on the eastern Skidegate Plateau and Queen Charlotte Lowland. Boggy forest and woodland are also widespread on sloping, windward terrain underlain by nutrient-poor, resistant bedrock, as over much of the Queen Charlotte Ranges portion of Moresby Island. These scrubby forests consist of mixtures of western redcedar, western hemlock, and often yellow-cedar, shore pine, and mountain hemlock as well. Salal, deer fern, spleenwort-leaved goldthread, false lily-of-the-valley Maianthemum dilatatum, bunchberry, Indian hellebore Veratrum viride, Nootka reedgrass Calamagrostis nutkaensis, and sedges (Carex spp.) are typical understory vascular species.

2.4 Subalpine vegetation

The subalpine zone on Haida Gwaii occupies elevations between about 600 and 800 m. Subalpine forests are not extensive but are distinctive, with dominance by mountain hemlock and yellow-cedar and open stands with relatively short, strongly tapered trees. Species of Vaccinium, false azalea, and copperbush Elliottia (Cladothamnus) pyroliflorus typically form the shrub understory, which is sparse (usually) to dense, depending on the openness of the canopy and the intensity of deer browsing. Subalpine forest thins out at yet higher elevations, into a parkland mosaic of tree clumps and heather meadows.

2.5 Alpine vegetation

Alpine vegetation occurs above 600–800 m and is concentrated in three areas: southwestern Graham Island, north-central Moresby Island, and the San Christoval Range south of Tasu on Moresby Island. An alpine heath of evergreen dwarf shrubs, especially white mountain-heathers (Cassiope spp.), yellow mountain-heather Phyllodoce glanduliflora, and partridgefoot Luetkea pectinata, is the dominant type of closed alpine vegetation. Herb-dominated alpine meadows are less common but very lush, with a variety of grasses (especially tufted hairgrass Deschampsia cespitosa), sedges (especially large-awned sedge Carex macrochaeta), and vigorous forbs. High-elevation rock outcrops, cliffs, boulder fields, talus slopes, wet runnels and gullies, and avalanche tracks have a sparse and discontinuous plant cover, but these rocky habitats support a rich flora that contains many of the rare vascular plant species of Haida Gwaii.

1 Nomenclature of vascular plants follows Douglas et al. (1998–2002).

2.6 Freshwater wetlands

Freshwater wetlands are among the most conspicuous features of the plant cover of Haida Gwaii (see Banner et al. 1988). Wetland classes widely recognized by ecologists and at least generally familiar to many people are bog, fen, marsh, and swamp. Flat and raised bogs cover extensive areas of the Queen Charlotte Lowland. Slope or blanket bogs are especially widespread on the windward Queen Charlotte Ranges, where in some areas they are essentially continuous from sea level to alpine. Both types of bogs are typified by stunted, shrubby conifers, evergreen-leaved shrubs, including common juniper Juniperus communis, Labrador tea Ledum groenlandicum, and western bog-laurel Kalmia microphylla ssp. occidentalis, several sedge-family species (cotton-grasses Eriophorum spp., tufted clubrush Trichophorum cespitosum, sedges), as well as pools with yellow pond-lily Nuphar lutea ssp. polysepala, numerous rills and streams, and Sphagnum peatmosses.

Fens also have peaty soils but are less acid and more nutrient-rich than bogs, and their vegetation is dominated by sedges, grasses, and often also shrubs such as hardhack Spiraea douglasii, sweet gale Myrica gale, Pacific crab apple Malus fusca, willows Salix spp., and Labrador tea. Marshes are also relatively rich in nutrients but occur on mineral sediments and support strictly herbaceous vegetation that is emergent from standing water. Sedge marshes are the most common type on Haida Gwaii. Fens and marshes are localized along flowing water and lake margins and are of minor extent, even on northeastern Graham Island, where they are most frequent. The "Pontoons" at the head of the Tlell River is the largest fen/marsh complex on the Islands.

Swamps are forested wetlands, rich in minerals and nutrients, but with moving rather than stagnant waters and mucky soils sufficiently aerated to support tall shrubs and trees. Conifer swamps are common on Haida Gwaii but are usually localized and do not dominate the landscape as do bogs. Dominant tree species are western redcedar, Sitka spruce, western hemlock, sometimes red alder Alnus rubra, and yellow-cedar at higher elevations. Skunk cabbage Lysichiton americanum is a very characteristic understory species of swamps, as is the liverwort Conocephalum conicum.

2.7 Maritime communities

Maritime terrestrial vegetation occurs on a variety of tidelands and uplands between the forest and the sea. Nonforested types restricted to the land–ocean interface include sand and shingle beach communities, rock and cliff communities, and tidal marshes. Calder and Taylor (1968) provide detailed descriptions of these vegetation types.

3. Pre-European vegetation

By "pre-European" vegetation, I mean the plant cover prior to first-hand, written historical accounts—that is, prior to 1850. My assumption is that the vegetation of Haida Gwaii then was much like that of temperate rainforest areas of southeast Alaska and of British Columbia's northern mainland coast now (Pojar and MacKinnon 1994; Alaback and Pojar 1997), except that it was relatively poor in species of vascular plants but had some endemic and otherwise phytogeographically interesting taxa (Schofield 1989; Taylor 1989; Brodo 1995). Paleobotanical studies indicate that the forests of Haida Gwaii "have existed in essentially their present form for the last 5,500 years or so, with the only significant natural change since then being the increased importance of red cedar during the past three millennia" (Mathewes 1989).

What is the "pristine benchmark," and how can we know? Following the argument of Jackson et al. (2001), we can recognize at least three partially overlapping periods of human impact on ecosystems: Aboriginal, colonial, and global. We are now in the global period, but most of the apparent change in Haida Gwaii forests took place in the colonial period—i.e., 1850–1970. Is it reasonable to assume that during the Aboriginal, pre-1850 period when only Haida were on the islands, impact on the vegetation was not great? Perhaps. Haida culture is marine-based. Presumably they would not have gone too far inland to harvest big trees, and their selective harvesting was consonant with the gap dynamics of the coastal forest. However, they have had lots of time, maybe 13 000 years (Hetherington 2002). And certainly 6000 (Duff 1964) to 15 000–20 000 people (Fedje et al. 2001) would have had a noticeable impact on native vegetation in and around villages, on shorelines and tidelands, and on selected species used as food, as medicine, or in technology (e.g., western redcedar, western yew). Evidently the Haida practised a form of agriculture, and not just with native species. They also cultivated potatoes and ate and traded them widely (Meilleur 2001). We remain uncertain about the role and extent of fire on Haida Gwaii. Wildfire seems to have played a minor role in shaping the vegetation (Banner et al. 1989). However, there are reports of Aboriginal burning along Skidegate Inlet (Turner 1999), and if it occurred there, it probably was practised elsewhere, especially near villages and in drier eastern areas—where there is some evidence in the form of charcoal in soil profiles and some of the forests have a suggestive age and structure.

4. Impacts of postindustrial humans[2]

Explorers such as Perez, Quadra, and La Pérouse glimpsed Haida Gwaii in the late 18th century, and soon the word spread that fortunes could be made trading with the Haida for sea otter pelts. No trading post or fort, however, was established on Haida Gwaii, and the sea otter and the fur traders vanished from the Islands during the early 1800s. The Islands experienced a minor gold rush in the 1850s, but no permanent white settlement resulted. There were other mining ventures (mostly for copper or coal close to tidewater) later in the 19th century, but proper settlements were not established until 1869, when the Hudson's Bay Company set up trading posts in Masset and Cumshewa Inlet. Christianity and more settlers arrived in the 1870s.

2 See Dalzell (1968, 1973).

The early 1900s saw a flurry of homestaking and townsite development, especially on eastern Graham Island. The major surviving settlements are Masset, Queen Charlotte City, Sandspit, and Port Clements, plus small settlements at Tlell, Lawn Point, and Skidegate Landing. Major Haida villages remain at Old Masset (Haida) and Skidegate.

Two whaling stations, one at Rose Harbour and another at Naden Harbour, operated for many years, from around 1910 to 1943. Salmon canneries existed in the early part of the 20th century at Alliford Bay, Naden Harbour, Lagoon Inlet, and Masset. There were cold storage and fish processing plants at Pacofi in Selwyn Inlet and in Rennell Sound, several salmon salteries, a crab cannery, a clam cannery, and kelp processing plants (one at Pacofi and another more recently at Nadu). Short-lived iron mines with fairly large workforces played out at Ikeda Bay, Jedway, and Tasu, all on Moresby Island.

Numerous logging camps have come and gone since 1910, including many small floating camps of the "gyppo" loggers. Terrestrial camps and extensive road networks were built at Cumshewa Inlet, Thurston Harbour, Masset, Juskatla, Moresby Camp, Sewell Inlet, Lyell Island, Eden Lake, and Rennell Sound, most resulting in temporary but intensive settlement.

Obviously, all of these settlements affected the native vegetation, directly and indirectly. Forests were cleared for homes, pastures, gardens, and stump farms; trees were cut for construction, pickets, firewood, corduroy roads, and so forth. Trails were hacked and roads were pushed through the bush. Domestic animals were brought to the Islands, and some went feral—like the wild cows of Naikoon Park—with impacts on vegetation that can only be guessed. Alien species were introduced, plants as well as animals. At first glance, it appears that settlement and the persistence of a sparse but aggregated human population have had mostly local effects on the plant life of Haida Gwaii. A closer look, however, reveals some extensive impacts—in the form of roads and access, introduced species, and consumption of energy and natural resources—that collectively define the rather large "ecological footprint" (Wackernagel and Rees 1996) of the resident and nonresident human population.

Present-day old-growth forests are in no way pristine and could be called "unnatural." Sometimes drastic changes, even in recent times, happen so fast that the memory of what used to be fades quickly (Golumbia and Rowsell this volume). Most people who now live on Haida Gwaii have never seen the original predeer forests, and it can be difficult for them (and others) to visualize or comprehend what it was like or even could be like. There seems to be a similar inability to comprehend preindustrial, order-of-magnitude-larger runs of salmon or the previous abundance of marine mammals, seabirds, and other marine animals.

Literature cited

Alaback, P.A.; Pojar, J. 1997. Vegetation from ridgetop to seashore. Pages 69–87 *in* P.K. Schoonmaker, B. von Hagen, and E.C. Wolf (eds.), The rainforests of home: profile of a North American bioregion. Island Press, Washington, D.C.

Banner, A.; Pojar, J.; Trowbridge, R. 1983. Ecosystem classification of the Coastal Western Hemlock Zone, Queen Charlotte Island Subzone (CWHg), Prince Rupert Forest Region, British Columbia. Unpublished report, B.C. Ministry of Forests, Smithers, B.C. 255 pp.

Banner, A.; Hebda, R.J.; Oswald, E.T.; Pojar, J.; Trowbridge, R. 1988. Wetlands of Pacific Canada. Pages 305–346 *in* National Wetlands Working Group, Wetlands of Canada. Ecological Land Classification Series No. 24, Environment Canada, Ottawa, Ontario.

Banner, A.; Pojar, J.; Schwab, J.W.; Trowbridge, R. 1989. Vegetation and soils of the Queen Charlotte Islands: recent impacts of development. Pages 261–279 *in* G.G.E. Scudder and N. Gessler (eds.), The outer shores. Queen Charlotte Islands Museum Press, Skidegate, B.C.

Barbour, M.G.; Billings, W.D. (eds.). 1988. North American terrestrial vegetation. Cambridge University Press, Cambridge, U.K. 434 pp.

B.C. Parks. 1992. Guide to ecological reserves in British Columbia. Ecological Reserve #45 V.J. Krajina (2-45A), Ecological Reserve #93 Lepas Bay (2-93A). Planning and Conservation Services, B.C. Parks, Victoria, B.C.

Brodo, I.M. 1995. Lichens and lichenicolous fungi of the Queen Charlotte Islands, British Columbia, Canada. 1. Introduction and new records for B.C., Canada and North America. Mycotaxon LVI: 135–173.

Brown, A.S. 1968. Geology of the Queen Charlotte Islands, British Columbia. Bulletin 54, B.C. Department of Mines and Petroleum Resources, Victoria, B.C. 226 pp.

Brown, A.S.; Yorath, C.J. 1989. Geology and non-renewable resources of the Queen Charlotte Islands. Pages 3–26 *in* G.G.E. Scudder and N. Gessler (eds.), The outer shores. Queen Charlotte Islands Museum Press, Skidegate, B.C.

Calder, J.A.; Taylor, R.L. 1968. Flora of the Queen Charlotte Islands. Part 1. Systematics of the vascular plants. Monograph No. 4, Research Branch, Department of Agriculture, Ottawa, Ontario. 659 pp.

Dalzell, K.E. 1968. The Queen Charlotte Islands, 1774–1966. Vol. 1. C.M. Adam, Terrace, B.C. 340 pp.

Dalzell, K.E. 1973. The Queen Charlotte Islands. Book 2: Of places and names. Cove Press, Prince Rupert, B.C.

Douglas, G.W.; Meidinger, D.; Pojar, J. 1998–2002. Illustrated flora of British Columbia. Vols. 1–8. B.C. Ministry of Environment, Lands and Parks and B.C. Ministry of Forests, Victoria, B.C.

Duff, W. 1964. The Indian history of British Columbia. 1: The impact of white man. Memoir No. 5, Anthropology in British Columbia. B.C. Provincial Museum, Victoria, B.C.

Environment Canada. 1980. Canadian climate normals, 1951–1980. Temperature and precipitation, British Columbia. Atmospheric Environment Service, Downsview, Ontario. 268 pp.

Fedje, D.; Sumpter, I.; Morton, J. 2001. Gwaii Haanas archaeological resource description and analysis. Unpublished report, Gwaii Haanas National Park Reserve and Haida Heritage Site, Queen Charlotte, B.C. 150 pp.

Hetherington, R. 2002. Interdisciplinary insights into paleoenvironments of the Queen Charlotte Islands/Hecate Strait region. Ph.D. thesis, University of Victoria, Victoria, B.C. [abstract in Canadian Geomorphology Research Group Bibliography Database].

Jackson, J.B.C.; Kirby, M.X.; Berger, W.H.; Bjorndal, K.A.; Botsford, L.W.; Bourque, B.J.; Bradbury, R.H.; Cooke, R.; Erlandson, J.; Estes, J.A.; Hughes, T.P.; Kidwell, S.; Lange, C.B.; Lenihan, H.S.; Pandolfi, J.M.; Peterson, C.H.; Steneck, R.S.; Tegner, M.J.; Warner, R.R. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293: 629–638.

Lertzman, K.; Spies, T.; Swanson, F. 1997. From ecosystem dynamics to ecosystem management. Pages 361–382 *in* P.K. Schoonmaker, B. von Hagen, and E.C. Wolf (eds.), The rainforests of home: profile of a North American bioregion. Island Press, Washington, D.C.

Mathewes, R. 1989. Paleobotany of the Queen Charlotte Islands. Pages 75–90 *in* G.G.E. Scudder and N. Gessler (eds.), The outer shores. Queen Charlotte Islands Museum Press, Skidegate, B.C.

Meilleur, H. 2001. A pour of rain: stories from a west coast fort. Raincoast Books, Vancouver, B.C.

Pojar, J.; Broadhead, J. 1984. The green mantle. Pages 49–71 *in* Islands at the edge. Douglas & McIntyre, Vancouver, B.C.

Pojar, J.; MacKinnon, A. 1994. Plants of coastal British Columbia, including Washington, Oregon and Alaska. Lone Pine Publishing, Vancouver, B.C. 527 pp.

Schofield, W.B. 1989. Structure and affinities of the bryoflora of the Queen Charlotte Islands. Pages 109–119 *in* G.G.E. Scudder and N. Gessler (eds.), The outer shores. Queen Charlotte Islands Museum Press, Skidegate, B.C.

Schoonmaker, P.K.; von Hagen, B.; Wolf, E.C. (eds.). 1997. The rainforests of home: profile of a North American bioregion. Island Press, Washington, D.C.

Taylor, R.L. 1989. Vascular plants of the Queen Charlotte Islands. Pages 121–125 *in* G.G.E. Scudder and N. Gessler (eds.), The outer shores. Queen Charlotte Islands Museum Press, Skidegate, B.C.

Turner, N.J. 1999. "Time to burn." Traditional use of fire to enhance resource production by aboriginal peoples in British Columbia. Pages 185–218 *in* R. Boyd (ed.), Indians, fire, and the land in the Pacific Northwest. Oregon State University Press, Corvallis, Oregon.

Wackernagel, M.; Rees, W.E. 1996. Our ecological footprint: Reducing human impact on Earth. New Society Publishers, Gabriola Island, B.C.

History and current status of introduced vertebrates on Haida Gwaii

Todd Golumbia, Lisa Bland, Keith Moore, and Patrick Bartier

Abstract

Many vertebrate species have been introduced to Haida Gwaii (Queen Charlotte Islands, British Columbia), particularly since the turn of the 20th century. A complete record of the history of faunal introductions on Haida Gwaii has not been compiled to date and is necessary for future work on introduced species management and for consistency when communicating this information to the public. This paper focuses on the history of mammal introductions, with some additional information on birds and amphibians. Although over 20% of the vascular flora and a large number of nonvascular flora are also considered introduced, this paper does not attempt to describe these. However, the potential risks associated with many of these plant species with respect to their invasive nature have been addressed to some extent by Engelstoft and Bland (2002) and Simberloff (this volume). The information contained herein is based on existing documents, reports, memoirs, and interviews of long-time residents. All confirmed sightings and distribution data have been digitized and are compiled in a Geographic Information System database. This database provides a baseline for tracking species distribution trends. Cases where existing information is incomplete or uncertain are outlined, and recommendations are made for follow-up. Studies to date on the effects of introduced species on Haida Gwaii and an overview of current research, inventory, and management actions in regard to introduced species are presented.

1. Introduction

Around the turn of the 20th century, explorers and naturalists began documenting the native fauna of Haida Gwaii (Queen Charlotte Islands, British Columbia) (Osgood 1901; Cole and Lockner 1993). Many of the species observed exhibited endemic characteristics. There are more unique subspecies on Haida Gwaii than in any other equal-sized area in Canada, leading to their title as "The Canadian Galápagos" (Foster 1982). The area also supports an assortment of rare plants that are considered locally or regionally endemic, several of which exhibit disjunct distributions (Lindsey 1989). A review of literature and museum collections undertaken by Gwaii Haanas National Park Reserve and Haida Heritage Site has resulted in a biodiversity database for the Haida Gwaii region (terrestrial and nearshore marine) that includes more than 6800 species of flora and fauna. Almost 200 are considered a conservation concern (by the World Conservation Union, the Committee on the Status of Endangered Wildlife in Canada, and the B.C. Conservation Data Centre) and may be endemic to the region. At least 217 are considered alien species. Although this report is restricted to introduced vertebrates, there has also been considerable work done to document introduced vascular plant species. Of approximately 665 known species, almost 25% are introduced (Calder and Taylor 1968; Taylor 1989; Lomer and Douglas 1999).

The 13 native mammal taxa (11 species, 2 with 2 subspecies each) (Table 1) of Haida Gwaii make up a relatively depauperate fauna. Several are considered endemic at the subspecific level (Burles et al. 2004). By comparison, 20 additional species occupy the adjacent mainland (McTaggart-Cowan 1989). Haida Gwaii is home to 280 species of birds (Hamel and Hearne 2001), including four subspecies of resident forest birds considered endemic to the islands. The archipelago is the main nesting ground in Canada for several marine birds of the northeast Pacific (McTaggart-Cowan 1989) and is internationally recognized for its seabird populations.

The introduction of nonnative species to Haida Gwaii has been relatively recent compared with the many thousands of years during which the native flora and fauna have evolved in isolation. In many cases, nonnative mammals were brought to the islands as a new source of food or as a means to generate income through trapping. Some animals were brought as pets or may have arrived accidentally. The Haida likely also played a role, either deliberate or accidental, in helping to introduce species to the Islands on their trips by canoe to the mainland (Foster 1965; Golumbia 2001).

During the period of European settlement and industrial development in the late 18th century, domestic and wild plants and animals accompanied the settlers. There was little regard for the ecological risk involved, as most settlers found the familiarity of these species a comfort in foreign lands. Since European contact, 10 nonnative mammals have been introduced, resulting in almost half the mammal species present on the Islands today (Table 1). In addition, at least five species of domesticated mammals have established feral populations. The information for amphibians and birds is not as well documented, but at least two amphibian and three

Table 1
Native and introduced faunal species, including feral animals and excluding native avifauna

Native vertebrate fauna[a]	Introduced vertebrate fauna (earliest known date)
Black bear *Ursus americanus*	Rocky Mountain elk *Cervus elaphus nelsoni* (1929)
Caribou *Rangifer tarandus* (extinct)	European red deer *Cervus elaphus elaphus* (1918)
River otter *Lutra canadensis*	Sitka black-tailed deer *Odocoileus hemionus sitkensis* (1878)
Marten *Martes americana*	Raccoon *Procyon lotor vancouverensis* (1940s)
Ermine *Mustela ermina*	Beaver *Castor canadensis leucodontus* (1936)
Deer mouse *Peromyscus keeni* (two subspecies)	Muskrat *Ondatra zibethica osoyoosensis* (1924)
Dusky shrew *Sorex monticolus* (two subspecies)	Red squirrel *Tamiasciurus hudsonicus anuginosus* (1950)
Silver-haired bat *Lasionycteris noctivagans*	Black rat *Rattus rattus* (1908)
California myotis *Myotis californicus*	Norway rat *Rattus norvegicus* (1901)
Keen's myotis *Myotis keenii*	House mouse *Mus musculus domesticus* (1901)
Little brown bat *Myotis lucifugus*	Ring-necked Pheasant *Phasianus colchicus* (1913)
Northwestern toad *Bufo boreas*	House Sparrow *Passer domesticus* (1890)
	European Starling *Sturnus vulgaris* (1890)
	Pacific tree frog *Hyla regilla* (1933)
	Red-legged frog *Rana aurora* (2002)
	Feral cattle (1893)
	Feral goats (1976)
	Feral dogs (no date)
	Feral cats (no date)
	Feral rabbits (1884)

[a] Native fauna are listed at the species level.

bird species have been introduced or have arrived after being introduced on the adjacent mainland.

Some introduced species have remained in localized populations around human settlement, while other, more invasive species have spread throughout the entire archipelago. Several of the nonnative species with the widest range and most potentially destructive impacts on native flora and fauna have been studied, although many others have received little attention, and their effects on the environment are poorly understood. Management and control programs have been initiated for a few species, although these are complex and often controversial issues. The first recorded introduction was in 1792, only 20 years after the first recorded European contact, when three domestic pigs were introduced at Magee Sound (apparently on the west coast of Graham Island, but not a current name). Nothing was ever heard of the pigs again (Dalzell 1968). The British Columbia Game Commission considered introducing moose to the archipelago, although there is no indication that this ever went beyond a discussion (Province of British Columbia 1930). There were also recommendations made by the local rod and gun clubs to introduce species such as capercaille *Tetrao urogallus*, quail *Colinus virginianus*, ptarmigan *Lagopus mutus*, ibex *Capra ibex*, chamois *Rupicapra rupicapra*, thar *Hemitragus jemlahicus*, moose *Alces alces*, goats *Capra hirsutus*, and kodiak bears *Ursus arctos* (Robinson 1957).

A fox farm was established at Sandspit for a short time in the 1930s (J. Carmichael, pers. commun., 2002), and there was a mink farm established near Mayer Lake (E. Ross, pers. commun., 2002). There are also recollections of a second mink farm established around the same time and location (S. DeBucy, pers. commun., 2001, 2002). It is believed, in both cases, that when these farms were closed, the animals were killed for their furs and the owners left the Islands (S. DeBucy, pers. commun., 1989). The presence of mink *Mustela vison* or fox *Vulpes vulpes* farms remains unverified in the written records or government archives. However, there is a reference to mink being liberated in 1944 (Province of British Columbia 1944).

In more recent times, there were plans to introduce ferrets *Mustela putoria* to St. James Island to control the rats, and in the mid-1970s the British Columbia Fish and Wildlife Branch considered establishing mountain goats *Oreamnos americanus* for sport hunting on the peaks of Moresby Island (K. Moore, pers. commun., 2001). There have also been references to the introduction of the red-sided garter snake *Thamnophis sirtalis* in the vicinity of Port Clements during the late 1980s or early 1990s, although there has never been a confirmed sighting.

2. Approach

In this paper, the authors attempt to provide an accurate representation of the current state of knowledge with regard to introduced vertebrates on Haida Gwaii. Where detailed information is available, it is provided as a summary of local knowledge gathered through interviews, a summary of published materials, or a review of relevant records and files in government and private archives. During the compilation of this report, the Council of the Haida Nation developed a strategic plan for introduced species management on Haida Gwaii (Engelstoft and Bland 2002). As part of this process, several interviews were conducted. Where appropriate, supplementary information has been included here.

Using individual species accounts, this report will 1) describe the history and current understanding of distribution and status for each species; 2) summarize historic and current research, monitoring, and management

initiatives; 3) highlight data gaps; and 4) make recommendations for future work.

Each species account is based on a combination of oral history and written records. Initially, persons knowledgeable on species introductions were interviewed. These interviews were conducted on four occasions, by Keith Moore in 1989, Lisa Bland in 2001, Lyle Dick in 2001, and Keith Moore and Todd Golumbia in 2002. Where possible, this information was cross-referenced and corroborated with published and unpublished written documents in government and private archives.

All available records or sightings for introduced species have been georeferenced in a database created and maintained by Parks Canada Agency. Each record indicates the location, date, and species occurring in the observation, as well as the appropriate citation for the source. Records are also included in the database where documentation is available to indicate species absence (nondetection). Following the species accounts, a short discussion summarizes the material, and several recommendations are made for further work.

3. Species accounts

3.1 Ungulates

3.1.1 Rocky Mountain elk *Cervus elaphus nelsoni*

Background: As early as 1878, elk were "certainly known to exist about the north west point of the island, but very seldom killed and not followed inland" (Cole and Lockner 1993). These "elk" were most certainly the Dawson caribou *Rangifer tarandus dawsoni.* There were also reports of a "special breed of elk" hunted near Rose Harbour on Kunghit Island, although the dates of this occurrence are not clear (Hagelund 1987). There are no records of this in B.C. Game Commission documents, which would likely have mentioned it, as Kunghit Island was designated as a game reserve for the protection of waterfowl during this time (Province of British Columbia 1920) and as a refuge for deer (Province of British Columbia 1930). However, it is likely that the ship carrying elk north from Vancouver to Queen Charlotte City in 1929 or 1930 would have stopped in at Rose Harbour and may have left some elk there as well.

In 1929, six Rocky Mountain elk cows and two bulls from Buffalo Park, Wainright, Alberta, were introduced to Haida Gwaii. They were let off a freight boat in Queen Charlotte City, courtesy of Mr. J.B. Harkin, Commissioner, Canadian National Parks, Ottawa (Province of British Columbia 1929). Official reports from 1930 indicated that, upon release, one cow attempted to swim to Maude Island and drowned, while the other five cows survived and had young the following year, resulting in a total population of 12 animals. An additional eight animals were brought to the Islands from Penticton in 1930 (Province of British Columbia 1930). Both of these introductions were well remembered by local residents (E. Piket, pers. commun., 1989; S. DeBucy, pers. commun., 2001; J. Carmichael, pers. commun., 2002; E. Ross, pers. commun., 2002). The Annual Report of the B.C. Game Commission in 1938 states that the elk were slowly increasing and were mostly found on Moresby Island, where conditions were believed more suitable than on the adjacent islands (Province of British Columbia 1938). Elk populations increased in the years after their introduction and ranged quite broadly on northern Moresby Island and southern Graham Island. By about 1948, the elk generally concentrated in the "Pontoons" (Tlell River) (S. DeBucy, pers. commun., 2002), on Moresby Island, and behind Queen Charlotte City until a bad winter around 1969 or 1970 killed off about 90% of them (G. Husband, pers. commun., 2001).

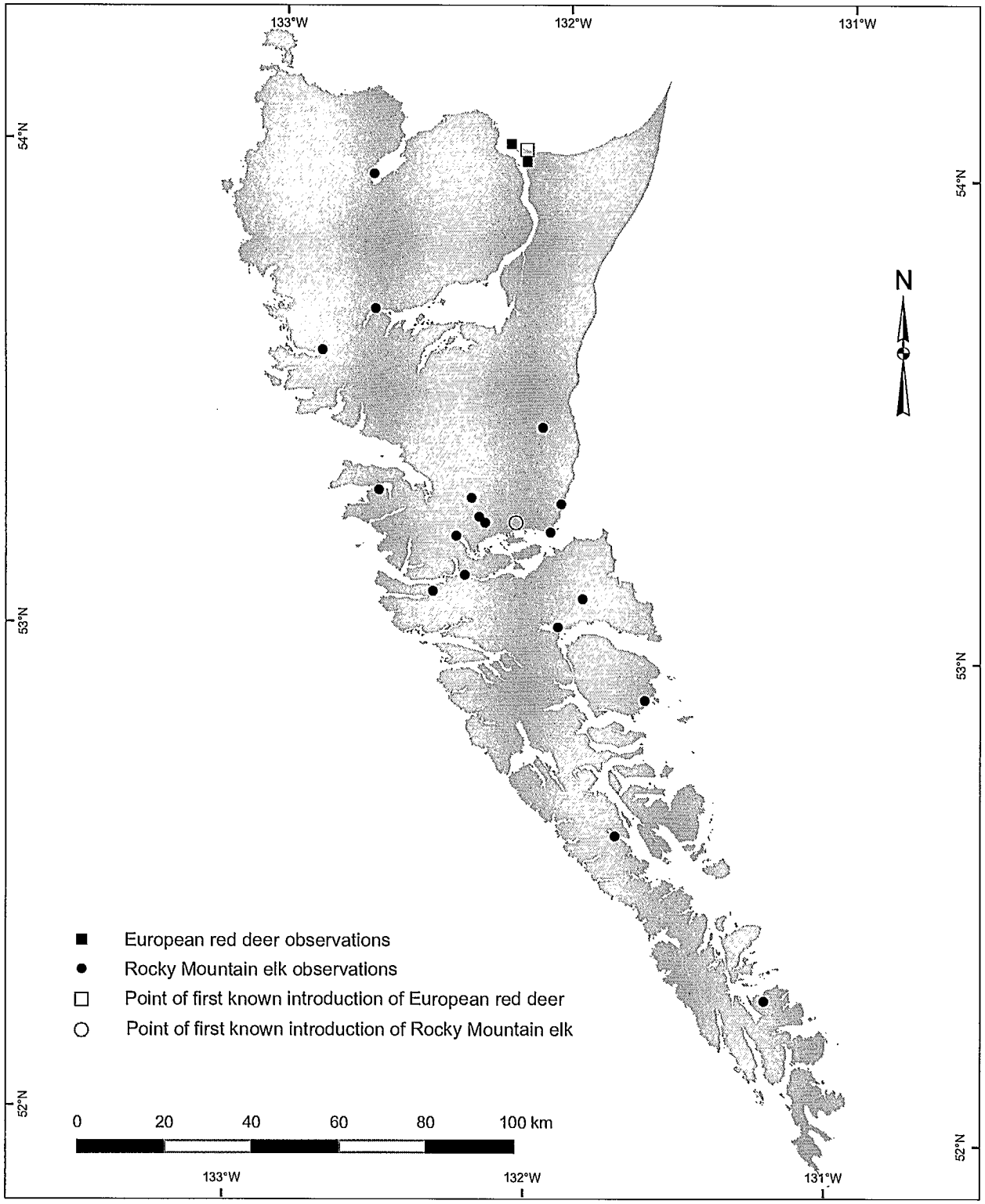
In response to local concern over the elk population, a study was done in 1975 to determine the Rocky Mountain elk's population status and ecology on Haida Gwaii (Trenholme and Hatter 1975). Elk sign indicated that they probably summered along creek beds, sheltering and feeding in small forest groves as well as feeding and occasionally bedding down in the Pontoons. Food for the elk was found to consist of spruce boughs, crab apple, alder, and grass, and, during critical winters in the Pontoons, the elk were known to feed on cedar (Trenholme and Hatter 1975). In the 1975 study, elk tracks and old droppings were seen in a Dawson Harbour ground survey, but the area was not considered to have any significant numbers (Trenholme and Hatter 1975). Local hunters reported elk sightings in locations such as Dawson Harbour, Chaatl Island, Rose Spit, Dinan Bay, Skidegate Lake, Skidegate Narrows, Slatechuck Mountain, Moresby Camp, Naden Harbour, and Jedway (Trenholme and Hatter 1975). The Pontoons and the area west of Naden Harbour were considered areas of high elk concentration at the time.

The 1975 study suggested that decreased elk numbers in the Pontoons were caused by a change in habitat. After the Pontoons burned in the early 1920s (S. DeBucy, pers. commun., 2002), the successional community of crab apple and willow, upon which the elk depended as a food source, became abundant. As forest succession continued, the crab apple and willow decreased, and the elk numbers began to decline. The introduction of the interior Rocky Mountain elk species rather than the coastal Roosevelt elk *Cervus canadensis roosevelti* found on Vancouver Island is also linked to the apparent poor success of the elk on Haida Gwaii (Trenholme and Hatter 1975).

Current distribution and population status: Elk continue to be limited in their distribution (Fig. 1) and have not expanded as rapidly and extensively as the Sitka black-tailed deer *Odocoileus hemionus sitkensis* (see below). It is believed that the majority of elk are currently concentrated in the Tlell watershed Pontoons, although there continue to be unconfirmed sightings of elk on Moresby Island in the vicinity of the Deena River flats, Moresby Camp, and Mosquito Lake (J. Hilgemann, pers. commun., 2002). The elk population is considered to be stable and is estimated to be anywhere from 40 to 100 animals (D. Richardson, pers. commun., 2001). It is possible that deer are playing a role in controlling elk distribution due to their abundance, which likely places a control on available food resources for elk.

Ecological impacts: Localized impacts of browsing and/or trampling have been observed, but no quantitative measurements have been made. The population

Figure 1
Map of Haida Gwaii indicating the known locations of Rocky Mountain elk and European red deer



is concentrated in the Pontoons, which is considered to be ecologically sensitive.

Current research and management initiatives: Two studies have been conducted to describe the local elk population. These are by Trenholme and Hatter (1975) and Spalding (1992). Since this time, there has been no work done locally, nor has there been any attempt to ascertain population numbers or trends.

Although numbers are considered low, hunting of bulls is allowed under regulation on Graham Island between 15 September and 15 November. On average, 8–10 animals are taken each year, and approximately 40–60 hunters participate (J. Hilgemann, pers. commun., 2002). Hunting is focused in the Pontoons area, and it is unknown how much, if any, hunting effort is undertaken in other areas of Haida Gwaii.

3.1.2 European red deer *Cervus elaphus elaphus*

Background: In the spring of 1918, four European red deer from New Zealand were transported to Haida Gwaii and introduced near Masset in the Delkatla flats (Fig. 1) (Province of British Columbia 1914; B.C. Game Commission 1956). By the time of their release, there were a buck, four does, and two fawns; a third fawn was born shortly after release (Province of British Columbia 1918). Apparently, these red deer were a threat to residents (one woman was knocked to the ground by a bull), so they were corralled and moved to the south side of Masset Inlet (Emmott 1918). By 1920, there were three does and two bucks still surviving, although they did not bear any fawns (Province of British Columbia 1920). The red deer dispersed widely across eastern Graham Island and northern Moresby Island (E. Ross, pers. commun., 2002). In the 1940s, Ronald Stewart, a police officer and game warden located in Masset, reported that the animals had formed a large herd. The local population declined abruptly during the years of World War II (1940–1944), attributed, by local residents, to overhunting by transient service personnel (B.C. Game Commission 1956; Carl and Guiguet 1972).

Current distribution and population status: Although red deer have been considered extinct on the Islands for some time, local sightings persist, and some think the red deer may have interbred with the Rocky Mountain elk (Spalding 1992). There are unconfirmed sightings of approximately 20 animals in the Blackbear River watershed on Graham Island (J. Hilgemann, pers. commun., 2002), as well as locations like Nadu Road, Cumshewa Inlet, and southern Moresby Island. Red deer and elk are capable of interbreeding and produce fertile offspring (Spalding 1992).

Ecological impacts: Unknown

Current research and management initiatives: None

3.1.3 Sitka black-tailed deer *Odocoileus hemionus sitkensis*

Background: The first introduction of deer to the Islands was by Reverend William Collison, who lived in Masset from 1876 to 1879. On one of his visits to the mainland, likely in 1878, he bought seven Sitka black-tailed deer from Tsimshian hunters and captured one additional deer on his voyage up the coast (Collison 1915). The Hudson's Bay Company carried them across to the Islands on its steamer free of charge, and they were introduced to Masset in 1878 (Dalzell 1968). By the next year, signs of them were seen as far as Skidegate (Osgood 1901), although they were not known to occur in Queen Charlotte City until 1928 (J. Carmichael, pers. commun., 2002). It is not clear when the deer crossed over to Moresby Island, although Osgood (1901) states that a deer was killed by hunters on Moresby Island prior to 1901. The deer near Masset thrived under the protection of Alexander McKenzie, an officer of the Hudson's Bay Company; after his death, however, they were apparently hunted out (Collison 1915), although this is not certain, and some likely remained through to 1911, when the next introduction of black-tailed deer occurred.

In the spring of 1911, the B.C. Game Commission felt that conditions were right for the establishment of a new game species on Haida Gwaii. Government contractors captured 28 deer at Porcher Island, near Prince Rupert, and sent them over to Haida Gwaii (Province of British Columbia 1914). Fifteen more Sitka black-tailed deer (two of which died) were sent over later in 1911; six were sent in 1912, and seven at the beginning of 1913.

More detail on the fate of these deer is provided in another account, indicating that 30 animals from Porcher Island were towed on a scow to Ship Island in Masset Inlet. Mr. Andy McCrea was given the job of caring for them and kept them on Ship Island for a month, after which he placed them a few at a time on different points where natural feed was good (McCrea 1976).

The last documented introduction of black-tailed deer occurred in 1925, when three mature bucks were captured near Price Island and released in Sandspit by Commodore Knight of the Royal Canadian Navy (Carl and Guiguet 1972).

Local people recall the incredible abundance of deer in the 1930s. They were valued for their meat and as a source of sport for hunters. Local resident George Husband recalls "thousands" of deer everywhere during this time, many in large herds (G. Husband, pers. commun., in Laskeek Bay Conservation Society 1998). If the deer were this abundant in the 1930s, it can be assumed that the 1878 introduction was successful, as typical growth rates (1.2–1.3) would have amounted to only 1500 deer following the 1911 introduction.

The "overabundant" deer became smaller, and many had warts, boils, and liver flukes (S. DeBucy, pers. commun., 2001). B.C. Game Commission reports suggest that deer suffered from disease but remained plentiful through the 1940s (Province of British Columbia 1948). This was followed by a massive die-off in the late 1940s (Robinson 1957), as deer were likely weakened by disease and then subjected to severe winter conditions in 1950. However, numbers were considered plentiful by 1951 (Province of British Columbia 1950, 1951) and overabundant in 1954 (Province of British Columbia 1954).

This pattern seems to illustrate an exponential growth period following introduction, followed by peak and crash population cycles based on a combination of food

shortage, weather, and disease. This pattern is complicated further in the mid-20th century as the rate of clearcut logging increased. According to locals, deer were once abundant in the muskeg areas, and, when logging increased, they moved into the slash areas (S. DeBucy, pers. commun., 2001). Their populations began increasing again in response to the abundance of forage in the clearcut areas following logging (S. DeBucy, pers. commun., 2001; D. Richardson, pers. commun., 2001).

The only observations found for the southern Islands indicate that deer were south of Hutton Inlet by 1937 (Hall, 1937) and on Kunghit Island by 1946, but did not likely arrive until after that date on SGang Gwaay (Duff and Kew 1958). Royal B.C. Museum staff who were at SGang Gwaay in 1957 reported the presence of deer (Duff and Kew 1958).

Current distribution and population status: There are few natural controls regulating deer numbers. The absence of predators found on the mainland and Vancouver Island (wolves or cougars), the mild climate, abundant food sources, and no browsing competitors have resulted in deer populations flourishing in the last century. The deers' ability to swim has allowed them to spread, and they now occupy virtually all the islands of Haida Gwaii, with only eight small offshore islands known to be deer free and two islands that have had deer populations greatly reduced (Table 2) (Golumbia 2000). There may be other islands with little or no impact by deer, although they have not been documented.

At present, population dynamics, density, and seasonal movements of deer on the archipelago are not fully understood. Martin and Baltzinger (2002) suggest a range of deer densities, from 13 to 30 deer/km^2, and 8500 km^2 of available habitat on the archipelago. This equates to population estimates ranging from 110 500 to 255 500 deer. On the two islands where deer depopulation occurred, cull data suggest minimum deer densities of 27–34 deer/km^2 (Gaston et al. this volume), which indicate that the offshore islands have much higher deer densities than the larger islands of Graham and Moresby.

Ecological impacts: The Sitka black-tailed deer has likely changed Haida Gwaii more dramatically than any other introduced species. Local resident George Husband said, "Before the deer spread to Moresby Island, early fallers would have to cut brush to get from one tree to the next, the salal was well over their heads" (G. Husband, pers. commun., in Laskeek Bay Conservation Society 1998). Early vegetation was also noted by Poole (1872) and Osgood (1901). In the 1950s, biologists observed many areas of overbrowsing and recognized the high density of deer along coastal areas and the relationship between early seral forests resulting from industrial logging and increasing deer numbers (Robinson 1957). Impacts on vegetation were noted on SGang Gwaay in 1957 (Duff and Kew 1958): "Recent over-browsing by deer has destroyed much of the shrubbery on the island. There are large areas devoid of living shrubs and the salal bushes are completely bare of leaves below a height of 4 to 5 feet." Scientists and foresters began taking more notice of the effects that deer were having on Haida Gwaii in the 1970s. As understanding of this issue increases, so too does the interest. When looking at deer overabundance worldwide, British researcher Robin Gill stated that the impact of deer on Haida Gwaii is as severe as that seen anywhere (Gill 1999).

There has been a dramatic reduction in the shrub and herb layers of many forest ecosystems on Haida Gwaii. Browsing by Sitka black-tailed deer has seriously depleted and sometimes eliminated western redcedar *Thuja plicata* and yellow-cedar *Chamaecyparis nootkatensis* regeneration in many mature forests as well as on logged sites (Banner et al. 1989). In areas that have been clearcut, few cedar seedlings grow into saplings and mature trees compared with spruce and hemlock. The number of cedar in the young forest is nowhere near what it would be in the absence of deer or what was in the original old-growth forest (Martin and Baltzinger 2002). Sitka spruce *Picea sitchensis* has been heavily browsed in forest openings, along beach edges, riverflats, and roadsides, and in former Haida village sites (Moore 1988; Vila et al. 2002, 2003). Various protection methods, such as Vexar tubing, are used by the forest industry to reduce browsing on young plantation cedar (Henigman and Martinz 2000).

Species that are known to be impacted by deer browsing include huckleberry (*Vaccinium* sp.), false azalea *Menziesia ferruginea*, salal *Gaultheria shallon*, salmonberry *Rubus spectabilis*, devil's-club *Oplopanax horridus*, sword fern *Polystichum munitum*, deer fern *Blechnum spicant*, Nootka rose *Rosa nutkana*, skunk cabbage *Lysichiton americanum*, Pacific crab apple *Malus fusca*, and foamflower *Tiarella trifoliata* (Banner et al. 1989; Laskeek Bay Conservation Society 1996). In particular, devil's-club and skunk cabbage populations have almost disappeared due to deer browse in forests (Pojar et al. 1980; Lewis 1982; Pojar and Banner 1984), and locals say deer have reduced the wild dune strawberries *Fragaria chiloensis* on Graham Island (D. Richardson, pers. commun., 2001). The presence of cloudberry *Rubus chamaemorus* on the muskeg has also been greatly reduced (B.C. Parks 1992). Populations of Nootka rose, Pacific crab apple, and western yew *Taxus brevifolia* were historically abundant along most of the shoreline (Chittenden 1884; Osgood 1901) and are now rarely seen. Many of these plant species have high cultural value to island residents.

Loss of foliage due to deer browse has been linked to a reduction in native insects (Allombert and Martin this volume) and in native birds due to a loss of nesting habitat, food sources, and protective cover. This leads to increased vulnerability to native predators (e.g., crows and

Table 2
Islands known to be deer free or from which deer have been removed

Island name	Size (ha)	Comments
Lost Island	10.4	
Low Island	8.5	
South Low Island	6.3	
Tar Islands (five)	23.0	
Deer-free total	48.2	
Reef Island	243.0	Deer removed in 1997–2001
SGang Gwaay	190.3	Deer removed in 1998–2001
Deer removed total	433.3	

ravens) (Martin et al. 2001; Martin and Joron 2003). The initial introduction of deer in 1878 may have altered habitat (Foster 1965) and/or brought disease to the Dawson caribou (J.B. Foster, pers. commun., 1989b). The caribou were believed to be extinct by the 1920s. Other linkages between loss of habitat and species reductions are expected in species such as the Haida ermine *Mustela ermina haidarum* (Burles et al. 2004).

Current research and management initiatives: Western Forest Products established several experimental deer exclosures in Sewell Inlet (Coates et al. 1985; Western Forest Products 1988; Bennett 1996) and on Ramsay Island (J. Barker, pers. commun., 1998). They have monitored the vegetation and subsequent deer browsing impacts. In 1996, the multidisciplinary Research Group on Introduced Species (RGIS) was formed to study the biological consequences of introduced species on Haida Gwaii. In 1997, RGIS organized a 5-year research project to examine the effects of the Sitka black-tailed deer and the red squirrel *Tamiasciurus hudsonicus anuginosus* on Haida Gwaii. Studies undertaken by RGIS deal with both direct impacts of deer browse on vegetation (cedar and understory plants) and related impacts of reduced insect fauna, reduced avifauna diversity, as well as increased nest predation.

In 2000, under the auspices of the British Columbia Ministry of Forests, a study was conducted to determine the range of potential options available to reduce deer browsing effects on Haida Gwaii. The report discusses social and economic values of deer, provides a summary of relevant scientific research, and outlines deer management options based on solutions used in other locations (Buck and Henigman 2000). Methods to census deer populations on the Islands were discussed, and local communities were consulted for their views. Responses from community groups, agencies, and individuals ranged from doing nothing to creating a commercial venison industry. Many Islanders depend on deer as an inexpensive and healthy food source; while most recognize the damage to vegetation and native habitat, the concept of eradication is untenable and deemed to be logistically impossible, except in small areas. Less drastic measures, such as population reduction, are considered by many to be more appropriate.

Regulated hunting started around 1930, at which time the bag limit was two bucks (J. Carmichael, pers. commun., 2002). An unlimited open hunting season was implemented in the 1950s in order to decrease deer numbers and improve the health of the deer (Province of British Columbia 1955, 1956; S. DeBucy, pers. commun., 2001). Regulated hunting was reinstated in 1976, and current hunting regulations on the archipelago are liberal, with a hunting season spanning 9 months of the year and a bag limit of 10 animals per hunter. Hunting is concentrated in the vicinity of the communities located on Graham Island and north Moresby Island and is generally heaviest where road access is available. In other areas of the archipelago, hunting pressure is minimal. Martin and Baltzinger (2002) showed that deer impact on the vegetation is higher where hunting is absent than where hunting pressure is high. Thus, hunting pressure appears to control deer numbers only in localized areas and only for a short time. Deer have become an integral part of the lifestyle on Haida Gwaii as a source of food, hunting sport, and scenic value.

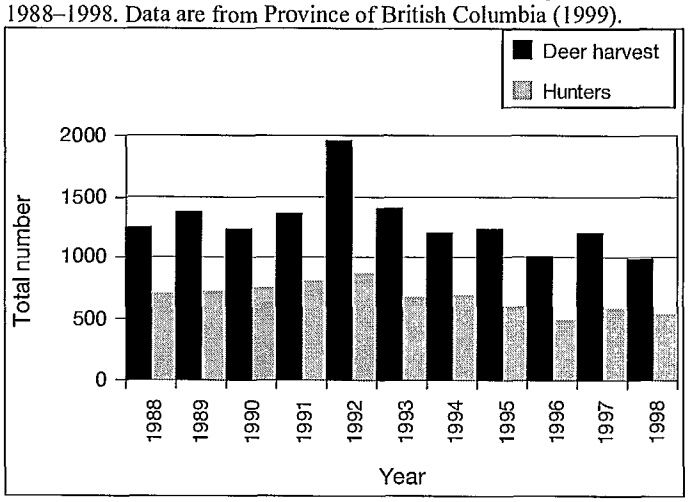
Hunting statistics for the period from 1988 to 1998 (Table 3) show annual harvest between 983 and 1942 deer, with an average annual harvest of 1286 animals, although this does not include harvest by Haida (Province of British Columbia 1999). Martin and Baltzinger (2002) suggest an estimated average of 1300 and 600 deer being taken annually on Graham Island and Moresby Island, respectively. Hunter effort has been relatively consistent over the period from 1988 to 1998 (Fig. 2), although it was higher in the past (Martin and Baltzinger 2002). Following designation under the *Canada National Parks Act*, hunting, except for traditional Aboriginal hunting, is prohibited in Gwaii Haanas, as in all national parks. However, due to the remote nature of Gwaii Haanas, it is unlikely that sport hunting would have any significant effect on deer abundance, as there are sufficient deer in more accessible areas to accommodate hunters.

Table 3
Deer harvest statistics for Haida Gwaii from 1988 to 1998[a]

	Number of deer harvested				
Year	Male adult	Female adult	Juvenile	Total	Number of hunters
1988	917	292	41	1 250	694
1989	965	382	23	1 370	705
1990	935	238	57	1 230	731
1991	1 022	286	37	1 345	804
1992	1 416	489	37	1 942	863
1993	988	383	28	1 399	657
1994	914	266	24	1 204	677
1995	908	289	35	1 232	588
1996	727	260	7	994	477
1997	832	347	17	1 196	572
1998	817	166	0	983	521
Total	10 441	3 398	306	14 145	

[a] Data are from Province of British Columbia (1999).

Figure 2
Total number of deer harvested and deer hunters for the period 1988–1998. Data are from Province of British Columbia (1999).



3.2 Small mammals

3.2.1 Raccoon *Procyon lotor vancouverensis*

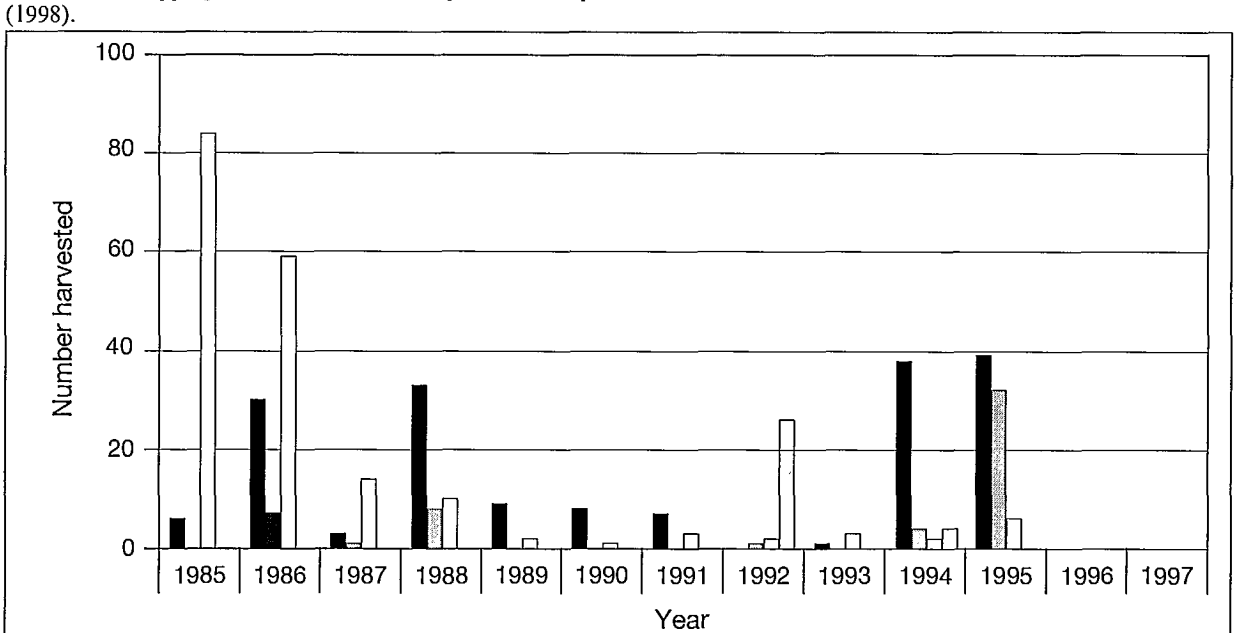
Background: The introduction of raccoons to Haida Gwaii occurred in the early 1940s, although the exact date is uncertain. Some sources say it was 1940 (Carl and Guiguet 1972), while local residents recall that it was sometime in the early 1940s. The animals were probably from near Campbell River, Vancouver Island (McTaggart-Cowan 1989), and were introduced to provide another source of fur for trappers. Local resident and long-time trapper George Husband (pers. commun., 1989) said that trappers asked the B.C. Game Commission for mink for their traplines but were told that the mink would be detrimental to seabirds. The Game Commission sent raccoons instead. The local game commissioner and police officer Sergeant Dunbar and local trapper George Husband released five or six near Jungle Beach at Lawn Hill around 1940 (G. Husband, pers. commun., 1989). Raccoons were likely released in several locations along the east coast of Graham Island between the Chinikundl and Tlell rivers. Although the raccoon hides were worth it initially, due to the American demand for "coon-skin hats" and the Japanese demand for hides, the market declined, and the demand for the pelts decreased (G. Husband, pers. commun., 2001).

Poor demand for pelts, along with low-quality furs (resulting from the mild climate), resulted in a lack of trapping pressure. With no natural predators, the raccoon population grew rapidly and spread over most of Graham Island, Moresby Island, and many of the smaller islands (Harfenist et al. 2000). It is believed that raccoons crossed from Graham Island to Moresby Island at Skidegate Narrows in 1958 (D. Gould, pers. commun., 1989). Raccoon populations were thought to be a lot higher in the past, and raccoons were once seen everywhere along the beach (G. Husband, pers. commun., 2001). From 1985 to 1997, 186 raccoons were harvested by licensed trappers (Fig. 3), although most of these were trapped in the 1980s, with only 19 animals recorded since 1988.

Current distribution and population status: Several raccoon surveys have been undertaken in recent years (Powell 1988; Summers and Rodway 1988; VandenBrink 1992; Hartman 1993). These surveys are summarized by Harfenist et al. (2000) and indicate that raccoons have reached many islands and pose a threat to all islands within 1 km of a source area (Fig. 4). Raccoons are widely distributed but seem to be more abundant on shorelines than in interior forests or higher-elevation habitats. However, little is known about their distribution on the larger islands.

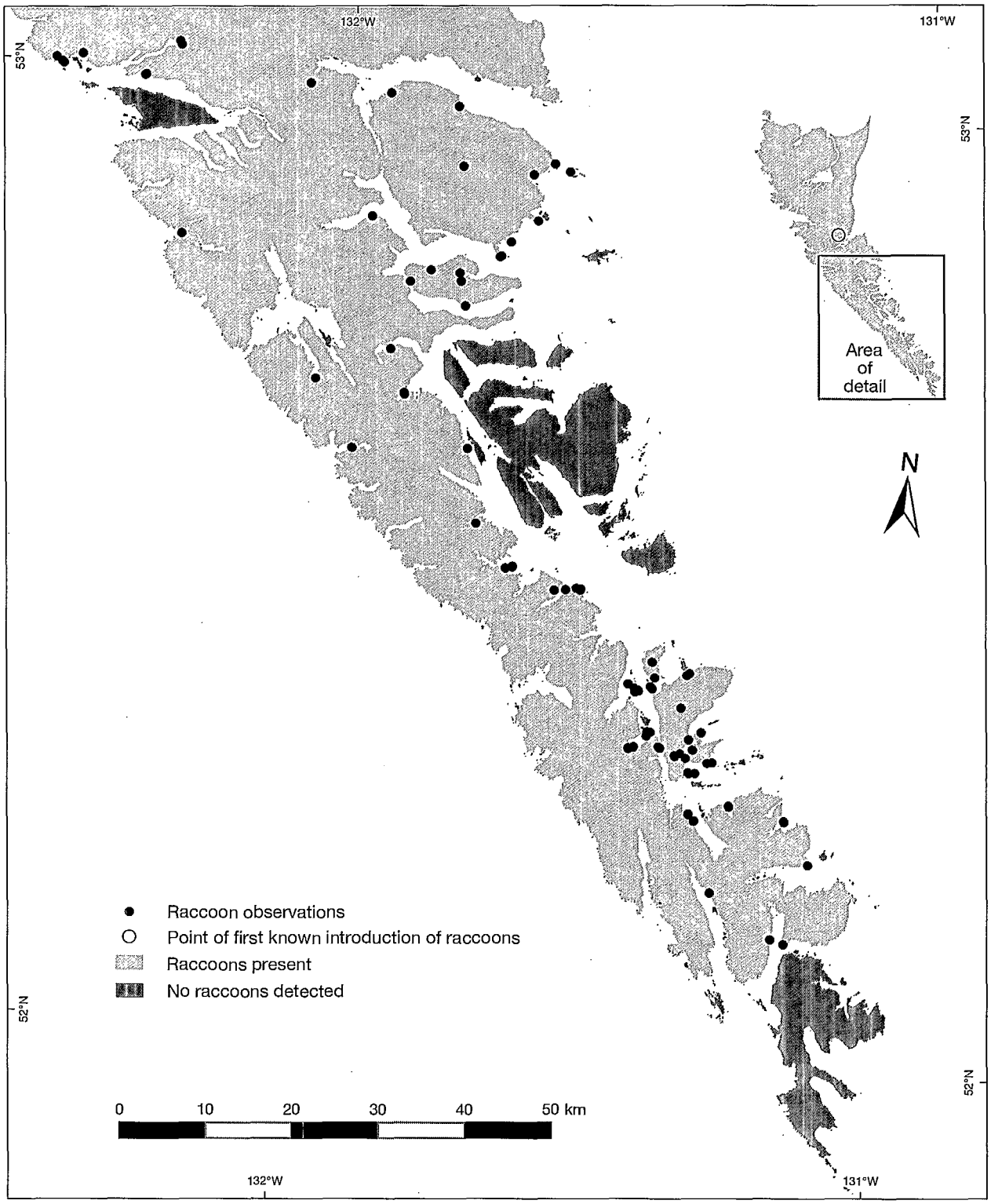
Ecological impacts: Raccoons have had an impact on seabird colonies, and studies have been undertaken to understand their effects. Seabirds have evolved to nest on islands inaccessible to the majority of predators. Of the 1.5 million seabirds breeding in Haida Gwaii, almost 100% nest in or on the ground. Although these birds have evolved

Figure 3
Haida Gwaii trapping records for introduced species for the period 1985–1997. Data are from Province of British Columbia (1998).



	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997
■ Beaver	6	30	3	33	9	8	7	0	1	38	39	0	0
□ Muskrat	0	7	1	8	0	0	0	1	0	4	32	0	0
□ Raccoon	84	59	14	10	2	1	3	2	3	2	6	0	0
▨ Squirrel	0	0	0	0	0	0	0	26	0	4	0	0	0

Figure 4
Map of Haida Gwaii indicating islands affected by raccoon



to avoid native predators by entering the nesting colonies at night, they are poorly adapted to nocturnal predators that are capable of entering or digging out the burrows. The results of a 3-year study initiated in 1989 found that about 80% of all Haida Gwaii seabird colonies and 75% of burrow-nesting seabird colonies are at high risk due to predation by raccoons (Hartman and Eastman 1999).

Raccoons have been implicated in the disappearance of seabirds on Helgesen and Saunders islands (Gaston and Masselink 1997) and in a population decline on East Limestone and West Limestone islands (Hartman et al. 1997). In some cases, nesting burrows are destroyed while eggs, chicks, and adult birds are eaten or sometimes just killed and left (Golumbia 2000). Raccoons feed in

freshwater, marine, and forest ecosystems. In lakes and streams, they feed on fish, snails, and frogs. Their impact on trout and salmon is unknown. In marine environments, localized reductions of shellfish and competition with native species in the rich intertidal zone are suspected impacts. Raccoon predation on the native northwestern toad *Bufo boreas boreas* in both Naikoon and Gwaii Haanas has been observed, as has predation on Red-throated Loons *Gavia stellata*, Sandhill Cranes *Grus canadensis*, and Canada Goose *Branta canadensis* nests (Reimchen 1993; Laskeek Bay Conservation Society 1996).

In summary, raccoons are wide-ranging and opportunistic, resulting in a wide range of ecological impacts, including impacts on burrow- and ground-nesting seabirds, shorebirds, herons, loons, geese, and cranes as well as intertidal organisms and the northwestern toad.

Current research and management initiatives: In 1995, the British Columbia Ministry of Environment, Lands and Parks, the Canadian Wildlife Service, British Columbia Parks, Parks Canada, the Council of the Haida Nation, and the Laskeek Bay Conservation Society developed a management plan and monitoring protocol to address raccoon presence in seabird colonies (Harfenist et al. 2000). A risk assessment was undertaken to focus monitoring and control of raccoons at selected seabird colonies (those at greatest risk). All raccoons discovered on the selected islands and on adjacent shorelines were eliminated, and results are indicating significant improvements to the conservation of seabirds and their habitats (Gaston and Masselink 1997). Although these control methods appear to be effective for seabird colonies, they require ongoing and continuous effort. Restoration of impacted colonies and the management of raccoon impacts on other species must still be addressed.

3.2.2 Beaver *Castor canadensis leucodontus*

Background: Haida Gwaii was officially identified as suitable for beaver as early as 1928 (Province of British Columbia 1928), although beaver may have been introduced "unofficially" at the Ain River in the 1920s by Ronald Stewart, the Masset police officer and game warden (D. Richardson, pers. commun., 1989). The first record of beaver introductions is verified as occurring in 1936, when six beavers were introduced to Graham Island by the B.C. Game Commission (Province of British Columbia 1936) in response to requests from local trappers. Although the location is not specified, it is believed that they were introduced at Ian Lake in the vicinity of Masset Inlet. The 1937 Annual Report of the B.C. Game Commission stated that the 1936 introduction of beaver was successful and recommended that an additional 3–5 pairs should be liberated on Graham Island (Province of British Columbia 1937). It was not until 1949 that the next shipment came. At that time, 11 beavers (3 females, 6 males, and 2 kits of undetermined sex) were live-trapped near Campbell River and released at Gold Creek near Mayer Lake (Sugden 1949). However, there were beavers in Gold Creek long before the 1949 introduction, and signs of them were seen as early as 1936 in the Pontoons area of the Tlell River (D. Richardson, pers. commun., 1989).

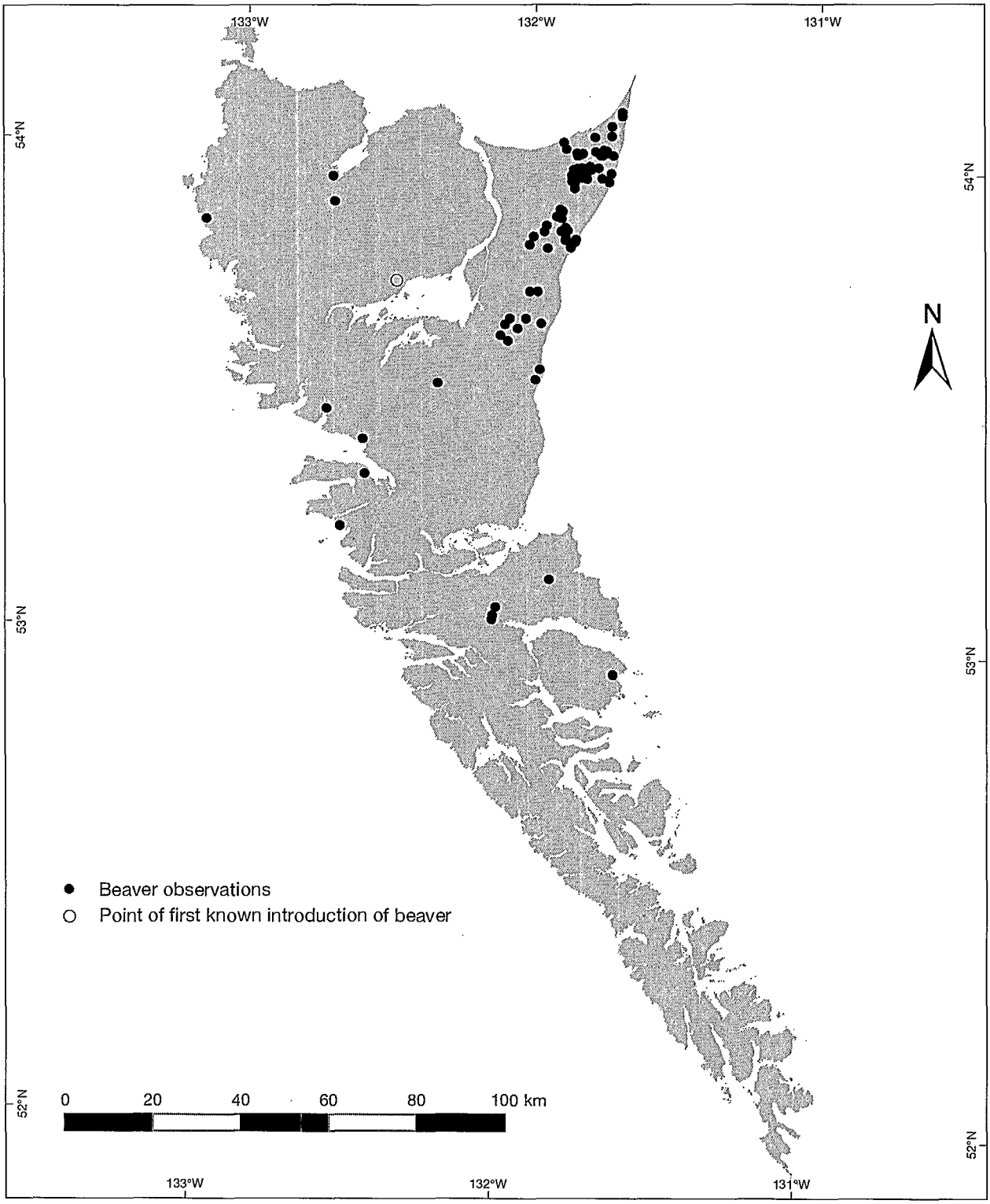
Current distribution and population status: Although formal surveys have not been undertaken, beaver are now thought to occupy virtually all low-lying areas of Graham Island and much of northern Moresby Island as far south as Louise Narrows (Fig. 5). They are most numerous in the Queen Charlotte Lowland—areas within and adjacent to Naikoon Provincial Park, including Nadu, Wotten, and Tlell rivers (Reimchen 1992; C. Marrs, pers. commun., 2001), and at isolated locations along the west coast of Graham Island. In 1986, beaver cuttings were observed at Waste Creek on Louise Island (Moore 1988), and a Gwaii Haanas National Park Reserve patrol reported old beaver sign in Upper Victoria Lake at the south end of Gwaii Haanas, although there are no confirmed sightings of beaver at either location (Columbia 2001).

Ecological impacts: Beaver feed on the inner cambium layer of red alder *Alnus rubra*, willow (*Salix* sp.), and Pacific crab apple on Haida Gwaii and then use the fallen trunks and branches to build their lodges (C. Marrs, pers. commun., 2001). They also eat cedar and have been observed to eat western yew. Beaver damage to yew trees has been noticed along the Tlell River, and a large yew tree felled by beaver was observed at the mouth of the Mamin River (L. Vigneault, pers. commun., 2001). Beavers also graze on various herbs, sedges, and shrubs. The combined effects of beaver and deer browse have reduced the willow and crab apple trees in several areas. The riparian area along the creek and surrounding Mayer Lake historically exhibited abundant crab apple trees. This area has been browsed and flooded by dams, and crab apple trees are now much less common (C. Marrs, pers. commun., 2001).

Beavers typically excavate banks to develop their burrows (C. Marrs, pers. commun., 2001), although recently beaver lodges have also been observed (L. Lee, pers. commun., 2001). They also create dams to increase and maintain water levels to facilitate access to food sources and burrows. Beaver dams have flooded some forested land, and higher water levels due to beaver activity can also change the course of streams, thereby disturbing riparian habitat for fish and nesting birds like the Red-throated Loon and Canada Goose (B.C. Parks 1999a). Some streams in Naikoon Park that formerly drained east now drain to the north (B.C. Parks 1999a). In some areas, beaver activity may increase fish habitat, as in the case of coho salmon *Oncorhynchus kisutch* rearing areas. However, beaver dams can create barriers to spawning salmon, especially to pink *O. gorbuscha* and chum salmon *O. keta*. In areas where beaver create dam after dam, fine organic debris settles into the area, creating siltation and low oxygen availability in prime salmon spawning habitat (C. Marrs, pers. commun., 2001).

Beaver have the potential to cause much damage on the Queen Charlotte Lowland (Banner et al. 1989). In areas where the gradient is low, a small dam of 30 cm can have a profound effect. Flooding raises the levels of small lakes, which submerge the adjacent forests and bogs, killing surrounding plants and trees, saturating the sphagnum (which lowers the pH), and producing profound changes in the ecosystem (C. Marrs, pers. commun., 2001). By building dams in the low relief of Naikoon Park, beavers are causing lakes to be joined that have likely remained separate since

Figure 5
Map of Haida Gwaii indicating the known locations of beaver observations



glaciation. Isolated species such as the endemic threespine stickleback *Gasterosteus aculeatus* could be threatened by the joining of once-distinct populations (Foster 1982).

Current research and management initiatives: Ten streams on northern part of Graham Island were studied to determine the presence or absence of fish in beaver-affected areas (C. Marrs, pers. commun., 2001). The North Graham Island Streamkeepers are working with B.C. Parks to protect crab apple trees with wire mesh exclosures on Mayer Lake. Future plans include studies on beaver populations to assess the extent of damage to crab apple trees (J. Gray, pers. commun., 2001). In Naikoon Park, beaver management strategies are a high priority because of their effect on the

Queen Charlotte Lowland (B.C. Parks 1999a). A small number of beaver are trapped (Fig. 3), but the number of individuals taken is likely insignificant.

3.2.3 Muskrat *Ondatra zibethica osoyoosensis*

Background: About 15 muskrats, probably from the Fraser River Delta, were released near Masset in 1924 by Mr. A.D. Hallett (McTaggart-Cowan 1989). Between the years of 1924 and 1934, locals also privately introduced muskrat (Pritchard 1934). In 1928, Ken Richardson and George Leary of Tlell transported eight muskrats into the Pontoons and released them (D. Richardson, pers. commun., 2001). In 1928 and 1929, the B.C. Game Commission's annual reports suggested that muskrats should be shipped over experimentally with a view of stocking the islands, although no records were found to suggest that further introductions were made (Province of British Columbia 1928, 1929). Resident Sergius DeBucy recalls that the muskrat introduced by Richardson and Leary were being trapped by 1933 (S. DeBucy, pers. commun., 2001). Muskrats were also trapped at North Beach and the Oeanda River area in the 1930s (E. Ross, pers. commun., 1989). There are accounts of another muskrat introduction by locals in 1930, when 12 animals were released in the Pontoons and in the Cape Ball area (D. Richardson, pers. commun., 1989), but this is uncertain.

Muskrat populations exploded in the 1930s. "Tlell and Queen Charlotte City were once hopping with muskrats; they were everywhere in people's dykes, gardens and wells" (S. DeBucy, pers. commun., 2001), and the tideflats and meadows in Tlell were riddled with muskrat holes, resulting in large areas caving in (D. Richardson, pers. commun., 2001). In the spring of 1933, the wisdom of introducing muskrats to Haida Gwaii was questioned when they were observed eating pink salmon fry at a fish enumeration fence (Pritchard 1934). After this population explosion, the population abruptly crashed in 1944–1945 (J. Carmichael, pers. commun., 2002).

The muskrat have not been studied to date, and the reason for the rapid population decline on Haida Gwaii is unknown. Many animals with deformities on their backs were observed when they were in high numbers (G. Husband, pers. commun., 2001; S. DeBucy, pers. commun., 2002).

In surveys conducted during 1957, muskrat were observed in the boggy areas of the Naikoon lowlands as well as in the Naden Harbour area and the mouth of the Copper River on Moresby Island (Robinson 1957).

Current distribution and population status: Although no formal surveys have been conducted, the population seems to have remained much lower than in the peak years around 1934–1935. There may be indications that muskrat numbers are increasing again, as muskrat runs around Mayer Lake are more noticeable than in previous years (C. Marrs, pers. commun., 2001). It is thought that muskrat occupy essentially the same area as beaver, but in fewer numbers (Moore 1988). Apart from Graham Island, muskrat have also been observed on Langara Island (McTaggart-Cowan 1989) but were never known there in significant numbers (Kaiser et al. 1997). They were likely eradicated from this site in 1996 during the rat eradication program (G. Kaiser, pers. commun., 2001). Current information indicates a restricted distribution in northern and eastern Graham Island and northern Moresby Island near Sandspit and at Pallant Creek (D. Burles, pers. commun., 2002) (Fig. 6). There is also one observation from 1989 citing the presence of muskrat at Breaker Bay on eastern Louise Island (J.-L. Martin, pers. commun., 2003).

Ecological impacts: Muskrats are known to feed mainly on grasses and reeds, and their direct impacts on riparian habitat are substantial (C. Marrs, pers. commun., 2001). There has been very little research undertaken locally on the muskrat.

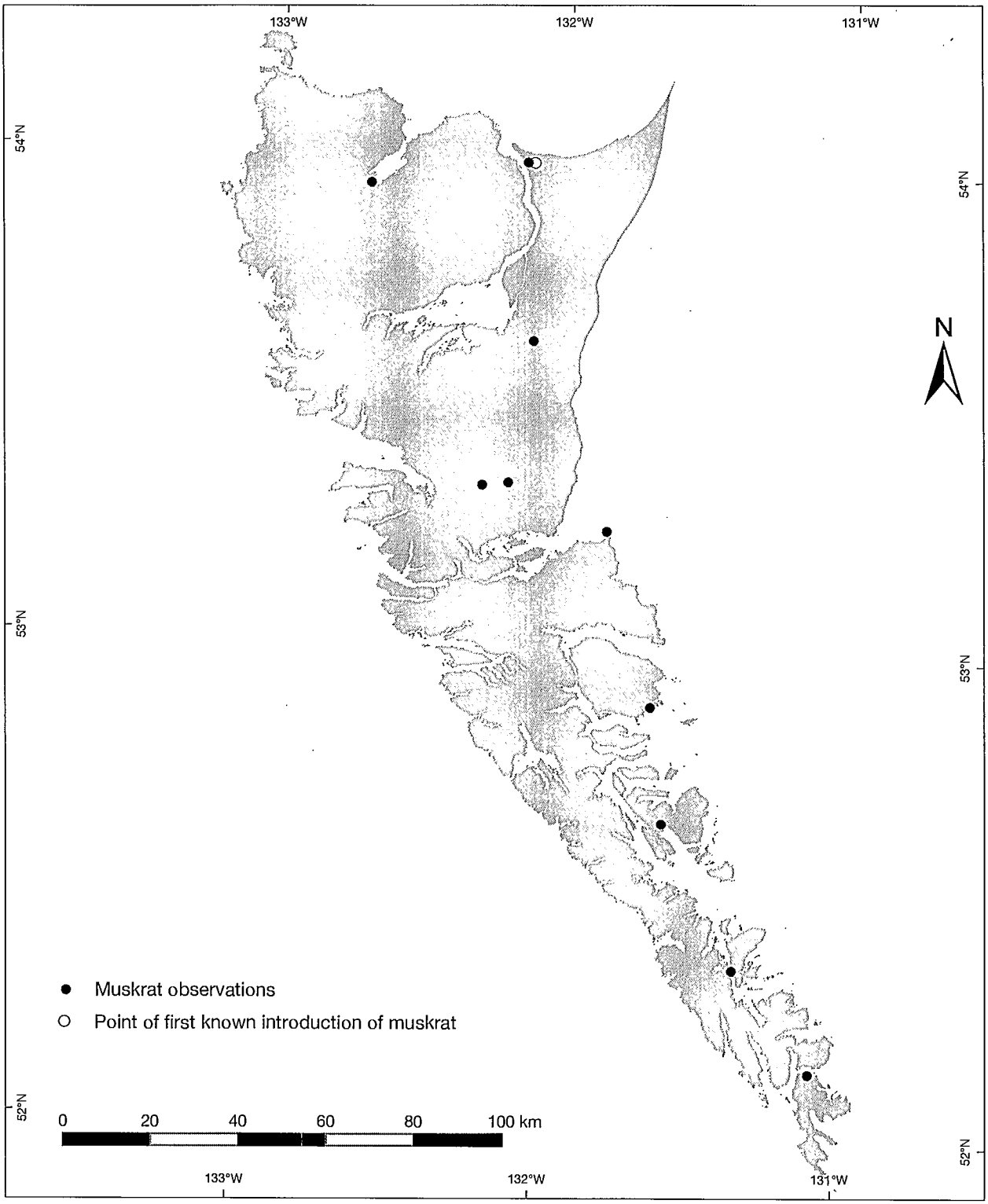
Current research and management initiatives: Muskrat are trapped in small numbers (Fig. 3). No other management initiatives are currently under way.

3.2.4 Red squirrel *Tamiasciurus hudsonicus anuginosus*

Background: Red squirrels were captured in the Sayward Forest near Campbell River and sent to the B.C. Game Commission for transmission to the Islands (McTaggart-Cowan 1989). These six squirrels were transported in 1950 (Carl and Guiguet 1972) and delivered to the local police officer and Game Commissioner, who released them in Queen Charlotte City (V. Fletcher, pers. commun., 1989). Squirrels were also possibly released to a number of remote islands (such as Lyell, Talunkwan, and Limestone) by the B.C. Forest Service to facilitate the collection of spruce cones and seeds used for silviculture, although a review of ministry files in Victoria did not provide any further detail, and it remains unclear as to the date and locations of these introductions and whether the B.C. Forest Service acted alone or in collaboration with the B.C. Game Commission. One additional piece of information provides details regarding the introduction of the red squirrel to Graham Island. In 1956, the Masset Rod and Gun Club made a formal request to the B.C. Game Commission for the release of squirrels in the Masset area. Justification for this release was to increase marten *Martes americana* prey and thereby increase marten numbers to provide trapping opportunities for local residents. It was also suggested that squirrel harvest of spruce cones would facilitate seed collection for nursery stock (Phillips 1956). Although it is not clear whether a translocation program was implemented, capture of squirrels already released in the vicinity of Skidegate and Queen Charlotte City for release in Masset was considered and may have been carried out by the District Game Warden (Walker 1956).

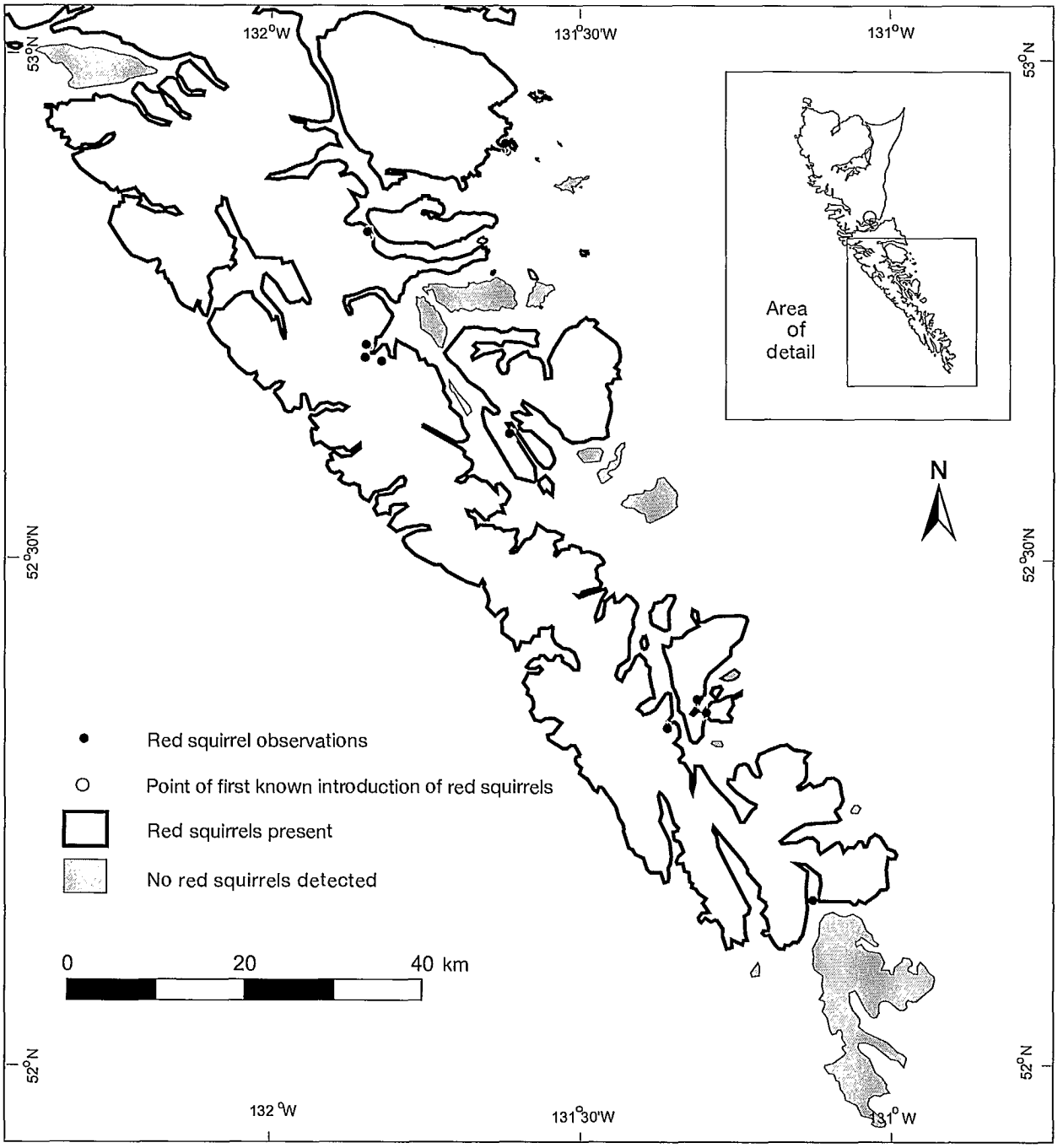
Current distribution and population status: Squirrels are now widespread on Moresby, Graham, and many smaller islands and are found as far south as Rose Inlet and Burnaby Island (Fig. 7, Table 4). As with other rodents, squirrels are very prolific, and their populations can erupt and expand rapidly, although their ability to expand across open water is unknown but expected to be low.

Figure 6
Map of Haida Gwaii indicating the known locations of muskrat



Ecological impacts: Marten populations were thought to rise soon after squirrels were introduced (D. Richardson, pers. commun., 2001). It has been hypothesized that the introduction of squirrels has provided the marten with an added source of prey, thus leading to an increase in the marten population (Moore 1988; Burles et al. 2004). In turn, biologists suspect that the increase in marten may have reduced the ermine population due to increased predation pressure (I. McTaggart-Cowan, pers. commun., *in* Moore 1988; Edie 2000). Squirrels are also effective predators on songbird nests, and squirrel predation may further aggravate the decline of songbird populations caused by deer impact on the vegetation (Martin, Allombert, and Gaston this volume).

Figure 7
Map of Haida Gwaii indicating the known locations of red squirrel



Current research and management initiatives: The RGIS has been conducting research to compare islands with and without black-tailed deer and red squirrel to understand the effects of squirrel predation and deer browse on songbird populations. From 1993 to 1996, artificial songbird nests were baited with quail eggs, and squirrel predation rates were compared between these and natural nests on islands with and without squirrels. The study has found that predation rates are highest on islands with squirrels and that the decrease in vegetation cover by deer has made nests more vulnerable to native avian predators (Martin et al. 2001; Martin and Joron 2003).

3.2.5 Black rat *Rattus rattus* and Norway rat *Rattus norvegicus*

Background: The black rat, also known as the European roof rat, ship rat, or Alexandrian rat, and the Norway rat are both known to occur on Haida Gwaii (Carl and Guiguet 1972; Bertram and Nagorsen 1995). Black rats probably arrived with the earliest European sailing ships and may have been on Haida Gwaii since the late 1700s and possibly earlier (Golumbia 2000). The species was first noted in 1908 (presumably in Masset), when black rats escaped from a ship beached for repairs (Harrison 1925). The larger and more aggressive Norway rat was known to occur

Table 4
Islands where squirrels have and have not been detected in the Gwaii Haanas region of Haida Gwaii[a]

Squirrels not detected	Squirrels detected
Agglomerate Island	Bischof Islands[b]
Bolkus Island	Burnaby Island
Frederick Island[c]	De la Bêche Island[d]
Helgesen Island[c]	East Limestone Island
Hippa Island[c,d]	Graham Island
Kunga Island	Huxley Island[b]
Kunghit Island[e]	Kat Island
Lihou Island[c,d]	Louise Island
Lost Island	Lyell Island
Low Island	Moresby Island
Murchison Island	Talunkwan Island
Ramsay Island[e]	Wanderer Island
Reef Island	West Limestone Island[d]
Richardson Island	
Skedans Islands	
South Low Island	
Tanu Island	
Tar Islands	
Titul Island[c]	

[a] Unless otherwise noted, the results are attributed to Martin (1995).
[b] D. Burles, pers. commun., 2002.
[c] A.J. Gaston, pers. commun., 2003.
[d] J.-L. Martin, pers. commun., 2003.
[e] Rodway et al. (1988).

locally by 1901 (Osgood 1901) but was not confirmed until 1981 on St. James Island (Bertram and Nagorsen 1995). In 1922, an early naturalist recounts the shooting of a Norway rat in a cabin where he was staying at Tow Hill (Patch 1922). There is also evidence of multiple introductions. On Kunghit Island, Guiguet (1946) indicated the presence of the black rat, while Harfenist (1994) identified the Norway rat. Similarly, on Langara Island, all records after 1988 have been of the Norway rat, which may indicate displacement of the black rat.

Current distribution and population status: Distributions for both rat species were described by Bertram and Nagorsen (1995). They found that rats inhabited 17 slands on Haida Gwaii. Rats have also been identified on four additional islands (D. Burles, pers. commun., 2002). Since 1995, rats have been eradicated from eight islands, with no subsequent detection (Kaiser et al. 1997; Golumbia 2002; D. Burles, pers. commun., 2004). The current distribution of both rat species is summarized in Table 5.

Ecological impacts: Langara Island historically supported one of British Columbia's largest seabird colonies (Gaston 1994). It is suspected that, since 1946, the declines of Ancient Murrelet *Synthliboramphus antiquus*, Cassin's Auklet *Ptychoramphus aleuticus*, Rhinoceros Auklet *Cerorhinca monocerata*, and Fork-tailed Storm-Petrel *Oceanodroma furcata* populations have resulted due to the presence of black rats (Gaston 1994). Black rats have since been replaced by Norway rats (Harfenist 1994). Ancient Murrelets on Langara Island have suffered a significant reduction in their population. Murrelet numbers were estimated at 50 000–90 000 breeding pairs in the 1970s (Gaston 1994). A comparative study between 1981 and 1988 indicated more than a 50% reduction in colony extent and a reduction of burrows of approximately 25%. Although the number of birds appeared to be increasing from 21 500 in 1981 to 24 100 in 1988, in comparison with the 1970s the overall decline was in the range of 54–75%. Continued decline of the Ancient Murrelets to fewer than 15 000 breeding pairs and the continued abandonment of former colony areas were documented by Harfenist (1994).

Rats may also have caused the disappearance of Langara Island's deer mouse *Peromyscus maniculatus* population. Reported as common in the mid-1930s, mice were considered to be absent by 1946. Impacts on native shrews and other bird species were also observed (Kaiser et al. 1997). It appears that rats on Kunghit Island have caused the endemic deer mice to evolve longer tails to facilitate their escape from rats (Foster 1965). Rats may also have caused reductions in the Cassin's Auklet and Ancient Murrelet colonies on Murchison and Lyell islands (Summers and Rodway 1988). Rodway et al. (1988) described rats as a significant predator of Ancient Murrelets at the Dodge Point colony on Lyell Island, where Lemon (1993) found a 25% decline in murrelet numbers. On St. James Island, Norway rats are believed to have caused the elimination of a Cassin's Auklet colony and a reduction in the Tufted Puffin *Fratercula cirrhata* colony (Bailey and Kaiser 1993). Reductions in colonies located on Kunghit Island have been attributed to rats as well (Harfenist 1994).

Current research and management initiatives: In 1993, the Canadian Wildlife Service initiated a rat eradication program on Langara, Cox, and Lucy islands using poison baits. The islands were baited at regular intervals until the eradication was complete. Except for an unexpected high mortality rate of Common Ravens *Corvus corax*, adverse effects on other island species were limited (Kaiser et al. 1997). In 1997, another eradication program was set up on Cape St. James (Golumbia 2000). Both eradication programs appear to have been successful, and it remains to be seen if the islands will remain rat-free and whether the bird populations will recover. Gwaii Haanas staff have developed a communication program to inform people about the risks of transporting rats from infested areas to noninfested areas on Haida Gwaii, and further eradication programs are planned for targeted islands in the protected area (Golumbia 2001). On Langara Island, monitoring continues, and owners of the fishing lodges located there are making efforts to prevent the reintroduction of rats (Taylor et al. 2000).

3.2.6 House mouse *Mus musculus domesticus*

Background: There is not much information available on the house mouse, but it is thought to have come to Haida Gwaii in the late 1800s and now is known to occur in every human settlement (Foster 1989a). In 1901, the house mouse was abundant at Clew and Skidegate villages, but introductions of cats were causing a decline in their populations (Osgood 1901). No studies have been done, and there are no indications that the house mouse has had a negative influence on the native biota (Foster 1989a).

Table 5
Summary of rat distribution on Haida Gwaii. Records in bold font are those islands where rats have been eradicated with no subsequent detection (X indicates presence; E indicates successful eradication). Unless otherwise noted, published reference is Bertram and Nagorsen (1995).

Name	Black rat	Norway rat	Rat spp.	Date observed (X) or eradicated (E)	Source (unpublished)	Reference
Bischof Islands		**E**		**2003**	**D. Burles, unpubl. data**	
Burnaby Island	X			1946	University of British Columbia	
Cox Island			X	1993	G.W. Kaiser, unpubl. data	
Cox Island			**E**	**1997**		**Kaiser et al. 1997**
Ellen Island			X	1999	D. Burles, unpubl. data	
Graham Island	X			1919	Canadian Museum of Nature	
Graham Island		X		1985	B.C. Provincial Museum	
Huxley Island	X			1992	D. Burles, unpubl. data	
Kunga Island			X	1998	R. Kelly, pers. commun.	
Kunghit Island	X			1946	University of British Columbia	
Kunghit Island		X		1993	B.C. Provincial Museum	Harfenist 1994
Kwaikans Island	X			1960	University of British Columbia	
Langara Island	X			1946	University of British Columbia	
Langara Island		X		1988	B.C. Provincial Museum	Bertram 1995
Langara Island	**E**	**E**		**1997**		**Kaiser et al. 1997**
Louise Island	X			?	?	
Lucy Island		X		1993	University of British Columbia	
Lucy Island		**E**		**1997**		**Kaiser et al. 1997**
Lyell Island	X			1960	University of British Columbia	
Moresby Island	X			1946	University of British Columbia	
Murchison Island	X			1960	University of British Columbia	
Park Island	X			1984	Rodway et al. 1988	
Shuttle Island	X			2002	D. Burles, unpubl. data	
St. James Island		X		1981	B.C. Provincial Museum	
St. James Island		**E**		**1998**	**Golumbia 2002**	**Golumbia 2002**
Swan Islands			X	1991	D. Burles, unpubl. data	
Talunkwan Island	X			1997	D. Burles, unpubl. data	
Tanu Island			X	1992	D. Burles, unpubl. data	

Current distribution and population status: Unknown

Ecological impacts: Unknown

Current research and management initiatives: None

3.3 Birds

3.3.1 Ring-necked Pheasant *Phasianus colchicus*

Background: In the spring of 1913, Charles Turney imported Ring-necked Pheasants and released them (Dalzell 1968). More birds were released by the B.C. Game Commission in the early 1920s, and a short open season was recommended for 1925 (Province of British Columbia 1925). Poor survival was attributed to predation of nestlings by crows (Young 1927). However, by 1946, pheasants had become very common in Tlell (Cook 1947), and they were hunted for years. It is believed that raccoon introductions caused their numbers to decline in the late 1940s (Dalzell 1968) and 1950s (S. DeBucy, pers. commun., 1989). A population of pheasants near the airport in Sandspit also disappeared around the same time. These declines may also have been due to disease or weather conditions (G. Husband, pers. commun., 2001). Several pairs of pheasants were released in widely separated parts of Haida Gwaii in 1966–1968 (Dalzell 1968; B.C. Parks 1992) and again in 1985 (B.C. Parks 1992).

Current distribution and population status: Pheasants were seen in Tlell as recently as the summer of 1999 but are thought to be absent now (D. Richardson, pers. commun., 2001). If still present, their numbers are limited and may not sustain a viable population.

Ecological impacts: Unknown

Current research and management initiatives: None

3.3.2 House Sparrow *Passer domesticus*

Background: The House Sparrow was introduced to North America in 1850 and likely reached British Columbia around 1890 (Campbell et al. 2001). It is common in areas of human habitation and does not occur in woodlands with

greater than 60% cover. It is known as a nuisance species and agricultural pest but provides ample prey for many raptor species (Campbell et al. 2001).

Current distribution and population status: The distribution of the House Sparrow is unknown for Haida Gwaii. However, it is noted as an accidental occurrence and is considered "essentially absent" from the Islands and the adjacent mainland coast (Campbell et al. 2001). Five observations have been recorded (Hamel and Hearne 2001), and the first breeding record for Haida Gwaii was recorded in Tlell (Engelstoft and Bland 2002).

Ecological impacts: Unknown

Current research and management initiatives: None

3.3.3 European Starling *Sturnus vulgaris*

Background: Very little information is known about introduced songbirds on Haida Gwaii. Following introduction in 1890, the starling spread across North America, arriving in British Columbia in 1945 (Campbell et al. 1997), and it has been documented on Haida Gwaii since the mid-1980s (Engelstoft and Bland 2002).

Current distribution and population status: Distribution is unknown, but numbers have been increasing dramatically since the birds' arrival (Engelstoft and Bland 2002). This species is common in the vicinity of local villages and open areas. It has been detected in Gwaii Haanas at Island Bay (westernmost island) in 1991 (J.-L. Martin, pers. commun., 2003) and at Hotspring Island in 1989 (A.J. Gaston, pers. commun., 2003).

Ecological impacts: Starlings have not been studied locally but are well recognized as a direct competitor for native species—particularly for competitive exclusion of secondary cavity nesters. Starlings are known as a nuisance bird in urban and suburban areas and have been implicated in declines of native species (Campbell et al. 1997).

Current research and management initiatives: None

3.4 Amphibians

3.4.1 Pacific tree frog *Hyla regilla* and red-legged frog *Rana aurora*

Background: Six frogs were brought to Moresby Island from Vancouver around 1933 (W. Mathers, pers. commun., in Reimchen 1991). These were released at Swan Lake, near Copper Bay. Local resident Dale Rennie collected two frogs and some tadpoles from the Port Coquitlam area and released them into Beaven's Pond (Graham Island), near Port Clements, in the summer of 1964. Between 1968 and 1970, frogs were taken from Beaven's Pond to Sandspit, where populations continued to expand (D. Rennie, pers. commun., 2001). By the 1970s, frogs were noticed on the Sandspit golf course, and by the 1980s, they were widespread (W. Mathers, pers. commun., 1989).

By 1966, Beaven's Pond had an abundant tree frog population. Frogs had spread as far as Woodpile Creek and to the Kumdis area of Port Clements, and in 1967, frogs were observed in Tlell, Juskatla, and Mayer Lake. Between 1973 and 1977, a local resident brought frogs to Queen Charlotte City from Miller Creek and remarked that they definitely were not there before then (F. Roberts, pers. commun., 1989).

In 2002, a second species, the red-legged frog, was identified in several locations near Port Clements and Juskatla (K. Ovaska, pers. commun., 2002). Some of the tadpoles brought in 1964 may have been of this species.

Current distribution and population status: Reimchen (1991) documented the spread and distribution of the tree frog throughout Graham Island and northern Moresby Island (see Fig. 8). There has been limited information gathered on the distribution of amphibians on Haida Gwaii, and no systematic surveys have been conducted.

Ecological impacts: The impact of the tree frog has not been studied, but there is some concern that it may be having a negative impact on the northwestern toad (Reimchen 1992; Burles et al. 2004).

Current research and management initiatives: Further study is required to determine the number of frog species present on the Islands and their present range and population status. There have been some observations of large tadpoles occurring at Mayer Lake, which could be green frog *Rana clamitans* or bull frog *Rana catesbeiana*, but this has not yet been confirmed (Engelstoft and Bland 2002). Red-legged frogs have been positively identified in the Juskatla and Port Clements areas (K. Ovaska, pers. commun., 2002), but their extent is unknown. Little is known of the effects of introduced frogs. They may be competing directly or indirectly with the native toad as well as with riparian or aquatic invertebrate populations. Interest in these ecological interactions will increase, as the western toad has been assessed as a species of special concern by the Committee on the Status of Endangered Wildlife in Canada and is listed under the federal *Species at Risk Act*.

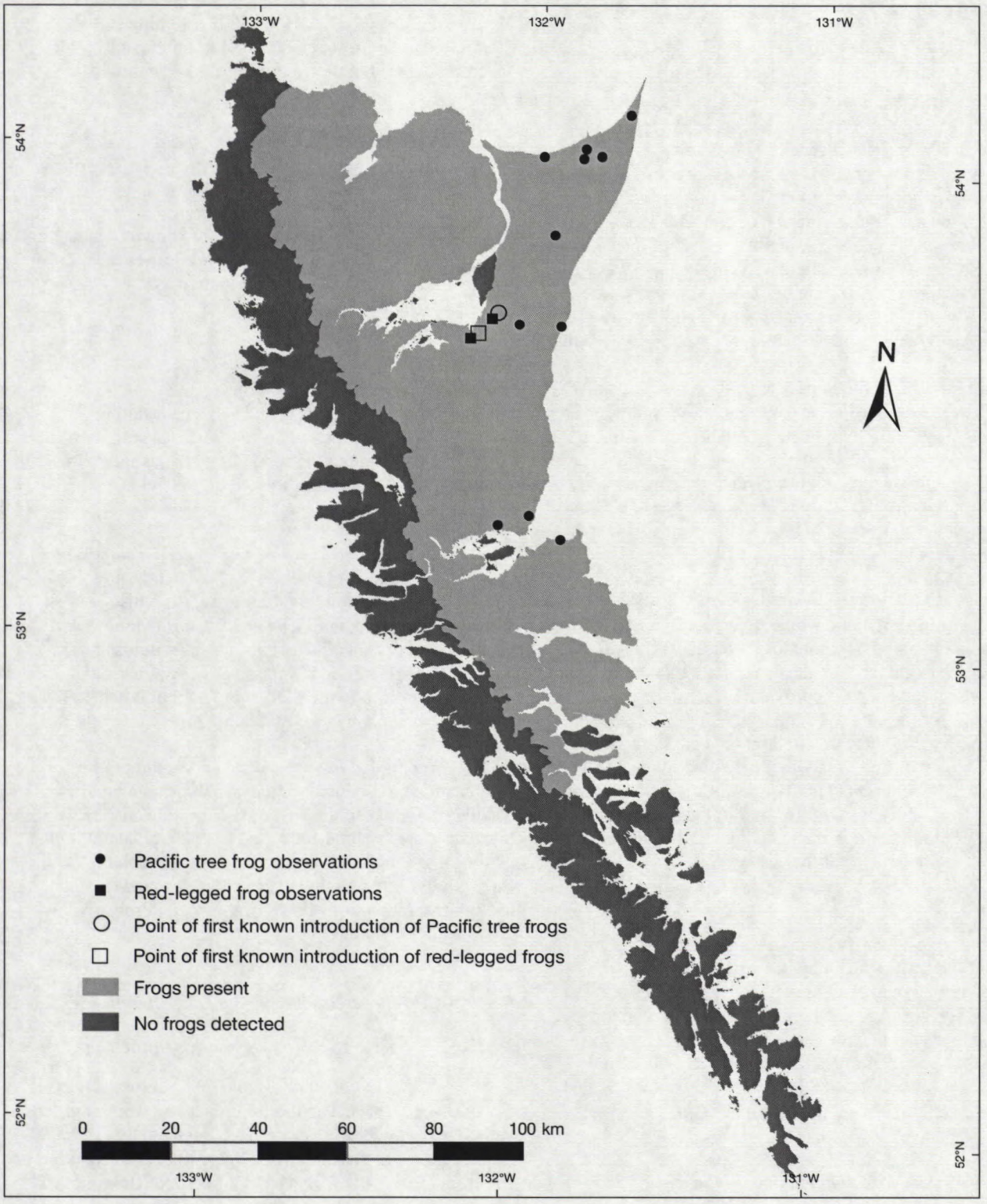
3.5 Feral mammals

3.5.1 Cattle *Bos taurus*

Background: Feral cattle were first abandoned in Masset around 1893 by Mr. J.M. Alexander (Dalzell 1968). Approximately 400 shorthorn cattle were originally to be transported back to the mainland. However, due to difficult weather and sea conditions encountered, the cattle were abandoned to roam the northeast beaches of Graham Island.

In 1919, settlers leased range by the Oeanda River, where their cattle grazed in the summer. The owners did not round them all up, and they joined the wild cattle (B.C. Parks 1999b). More recently, cattle abandoned at Cape Ball have joined up with the wild cattle, and now the mix of breeds includes shorthorn, Guernsey, Red Poll, Ayrshire, white Hereford, and some milk cows (D. Richardson, pers. commun., 2001).

Figure 8
Map of Haida Gwaii indicating the known locations of Pacific tree frogs and red-legged frogs



At every opportunity, early settlers shot these cattle for their meat (Patch 1922), and some attempts were made by "Mexican" Tom Hodges and other settlers to round up the wild cattle (Dalzell 1968).

Current distribution and population status: Based on a review of observational information, feral cattle herds appear to have a restricted distribution in the Queen Charlotte Lowland along the northeastern coastal portion of Graham Island. In a 1998 assessment of feral cattle by the B.C. Ministry of Forests and B.C. Parks, they were observed in the Tlell, Oeanda, and Cape Ball rivers and in Blue Danube and Bull swamps. Ministry of Forests staff observed 20 cattle in

the Blue Danube Swamp and 30 at the mouth of the Oeanda River. The cattle (unknown breed) were observed in groups of 18–20 and appeared to be healthy (B.C. Parks 1999b).

Ecological impacts: Wild cattle feed on grasses, sedges, shrubs, willow, and young spruce trees. They create protective galleries and barns in the forest, damage trees by rubbing, and have created trails, hummocks, and terraces in the Tlell River area (B.C. Parks 1999b). Long-term impacts may include changes in plant species composition due to browsing, trampling, and intensive grazing of certain plant species, such as the native dunegrass *Elymus mollis* and bluegrass (*Poa* spp.), and the spread of invasive exotic species. Heavy trampling may create changes in bog communities and destabilization of dune terrain (Madrone Consultants Ltd. 1992). There is also potential for impacts on the sensitive salt marsh vegetation at the Tlell and Cape Ball rivers.

About 80% of the impact on dune ecosystems in Naikoon Park is estimated to be caused by deer, and there is insufficient information to indicate whether feral cattle are a significant threat to natural populations or processes (B.C. Parks 1999b). Further research is considered a low priority, although a more thorough study is needed to assess impacts on plant species composition in bogs, dunes, and salt marshes and to assess population trends (Moore 1992).

Current research and management initiatives: If considered, removal of cattle would be difficult due to their aggressive nature and the remote locations they inhabit. Removal of the cattle through the use of hunters or culling programs would require the approval of several agencies (Moore 1992). Local interests suggest that leaving cows in Naikoon Park is warranted due to their historic significance to early settlement in the area. Others feel that hunters should be able to continue to hunt cows for meat (B.C. Parks 1999a). While hunting is permitted within the park, feral animals do not fall within British Columbia's *Wildlife Act*, so there is no hunting season for the cattle.

3.5.2 Goats *Capra hircus*

Background: In 1976, domestic goats were abandoned on Ramsay Island by homesteaders. Their numbers increased to approximately 20, and various government agencies became concerned and indirectly encouraged locals and fishermen to shoot them. Three were seen in 1984: two billies and a nanny (Moore 1988). The goats were still present in 1988 but are believed to have died out since then (L. McIntosh, pers. commun., *in* Burles and Gardiner 1991).

Current distribution and population status: Feral goats are not known at this time.

Ecological impacts: Goats are known to cause severe impacts on vegetation due to intense browsing pressure.

Current research and management initiatives: None

3.5.3 Dogs *Canis familiaris*

Background: Feral dogs have been found in Naikoon Park (B.C. Parks 1999a), but nothing is known of their numbers or present distribution. Small packs of dogs are also observed in the vicinity of the communities on Haida Gwaii.

Current distribution and population status: Current distribution is unknown, but it is expected that feral dogs are restricted to areas close to human settlement.

Ecological impacts: Dogs are known to harass and hunt deer. They can also be vectors for viruses and parasites that may be transmitted to native mammals.

Current research and management initiatives: None

3.5.4 Cats *Felis catus*

Background: Cats can have a devastating effect on songbirds, small mammals, and seabirds and are well recognized throughout the world as a serious threat to native fauna. They have been abandoned on several islands after their human hosts moved on.

Current distribution and population status: Feral cats occur around communities on the Islands, and there have been reports of them on Langara, Murchison, Lyell, Kunghit, Hotspring, and St. James islands (Moore 1988). Following the eradication of rats, cats are almost certainly gone from St. James and Langara islands. A cat was trapped and removed from Lyell Island in 1994, but it is unknown whether there are any cats remaining there.

Ecological impacts: Feral cats could pose a serious threat to seabird colonies, as they have in other island ecosystems in the world (Bailey and Kaiser 1993). Introduced by lighthouse keepers to Langara Island, feral cats likely caused mortality in Ancient Murrelet colonies in the early 1960s, although they were not mentioned as predators in studies through to 1989 (Bertram 1995). Probably any on Langara would have been exterminated during the rat eradication program.

Current research and management initiatives: None

3.5.5 Domestic rabbit *Oryctolagus cuniculus*

Background: Rabbits have been introduced to Haida Gwaii several times. The first introductions were reported in 1884 by Alexander McKenzie of Masset and by Reverend Robinson on Bare Island in Skidegate Inlet (Chittenden 1884). In 1913, Neil Walsh put four pairs of Belgium hares in his meadow at Tlell, and rabbits were considered locally abundant until the 1940s (Dalzell 1968). In the 1920s, a resident of Tlell had 0.2 ha of fenced land with rabbits. He eventually released them due to overcrowding; following this, in 1936, the rabbits were very abundant in Tlell (D. Richardson, pers. commun., 2001).

Rabbits may have died out due to hunting pressure, predation, or an inability to cope with the cold, damp climate. Belgian hares and Flemish giants were also

introduced unsuccessfully (D. Richardson, pers. commun., 2001). Rabbits were also introduced to Lyell Island in 1986 (K. Moore, pers. commun., 2001) and to Murchison Island but do not appear to have become established (Columbia 2001).

Current distribution and population status: A few rabbits are known to occur in the vicinity of both Lawn Hill and Tlell, but their population and distribution are not documented.

Ecological impacts: The impacts of rabbits on Haida Gwaii are unknown, but on other islands in the world they have been known to cause serious problems related to browsing of vegetation and burrowing (Moors and Atkinson 1984).

Current research and management initiatives: None

4. Conclusion

In most cases, little forethought went into the consequences of species introductions on Haida Gwaii; settlers were merely continuing the lives they had left behind on the mainland or another continent. With the exception of rats and mice (accidental introduction) and frogs (purposeful introduction), partnership with government was common in the introduction of vertebrates. Up until the 1960s, this was a key role of the B.C. Game Commission, and introductions were often in response to lobbying from local residents. Introduced species continue to provide a source of livelihood through trapping or hunting for food; while some species are universally seen as pests, others retain high value. The ecosystems of Haida Gwaii are changing due to the impact of introduced species. These changes may be pronounced and widespread or less obvious and localized, depending on the species and its range. Current research has provided a more definitive picture of some species, but in many cases our understanding is limited. The effects of deer, beaver, and raccoon are considered the most serious and widespread, while rats, muskrats, and feral cattle have had significant effects in more localized areas.

This compilation of historical records for species introductions helps to bridge the gap between recorded documentation and local knowledge. Both sources are relevant and important in piecing together this larger picture. Local memories are often the source of much insight. Scientific records and documented reports can provide a window in time from which to view the management philosophy of the day. Although this report attempts to be complete, there will continue to be a discovery of new information and perhaps new species, such as the red-tailed frog, which has likely been resident on the archipelago for some time but was identified only in 2002. There are several areas where missing information may be retrieved or where further study on introduced species could be undertaken. It is expected that historical accounts and research results will continue to come to light on various species. As a result, records will need to be revised and updated. The Parks Canada Agency database on introduced species distribution should be maintained and updated with all new information. To facilitate this and to ensure that the information is available to any interested parties, the database should be made accessible via the Internet. A similar compilation of data for introduced flora is being developed but requires further effort, particularly with regard to time and location of introduction and historic and current distribution. These records will be useful in tracking past, current, and future distributions, as well as eradication or restoration efforts.

Alternatives for management are often controversial. One could argue that over time, the introduction of species may be an inevitable step in the natural progression towards a more homogeneous global ecosystem. Ecological conditions could be allowed to evolve untouched with the hope that the introduced species will reach equilibrium. Yet to do nothing is contrary to the goal of maintaining biodiversity, since certain species may be eliminated (Columbia 2000). In the current age of enhanced global trade and free movement of goods and people around the globe, the future potential for species introductions is great. This era is being coined the Homogocene by many researchers with an interest in the global effects of introduced species (IUCN 2001).

The introduction of predators and other biological controls to eliminate introduced species in other parts of the world has often caused more problems than it has solved and in the present day is not considered a wise solution for Haida Gwaii. The Haida Gwaii landscape encompasses many different land management objectives, and these will influence any action regarding introduced species. Forestry, hunting, conservation, recreation, agriculture, and human habitation all play a role (Golumbia 2000).

Within Gwaii Haanas, management decisions are specific in relation to terrestrial, aquatic, and estuarine ecosystems, as noted in the Terrestrial Ecosystem Conservation Strategy (Golumbia 2001). Two of the three most important conservation issues are the effects of introduced deer on forest ecology and the effects of other introduced mammal predators on native mammals (Golumbia 2001).

The 1999 Naikoon Park Management Plan indicates several objectives related to introduced species. These include a desire to better understand native flora and fauna that are rare or threatened, to increase knowledge of the effects of introduced species—specifically feral cattle—on the ecosystem, to develop management plans for beaver and raccoons, and to provide regulated hunting for specific introduced species (B.C. Parks 1999a).

During the winter of 2000–2001, the Council of the Haida Nation and the B.C. Ministry of Water, Land and Air Protection commissioned a report to establish restoration priorities and strategies associated with the impacts of introduced species (Engelstoft and Bland 2002). This initiative also brought together interests and knowledge from discipline experts, land managers, and local people through a series of workshops and interviews. The report provides an overview of species introductions, a synthesis of local perspectives, and the framework for a strategic restoration plan. In many ways, the outcomes of this initiative and the RGIS conference have commonalities and complement each other well.

One of the significant outcomes of the RGIS symposium and workshop (Golumbia and Rowsell this volume) was the formation of an introduced species task force. This transition to a locally based lobby and action group will maximize the likelihood that this initiative will continue to build momentum and result in some concrete restoration actions on the ground.

Acknowledgements

Some of the information in this paper comes from literature sources, but much of it has been gleaned from local residents and people who have worked on the Islands over the years. Without their enthusiasm in providing recollections and interpretations of current information, this paper would have far less value. For delving into the provincial archives and government files, we thank Lyle Dick, Historian, Vancouver Service Centre, Parks Canada Agency. The database of species sightings and references was designed and compiled by Pat Bartier and Lynda Melney (Gwaii Haanas staff).

Literature cited

Bailey, E.P.; Kaiser, G.W. 1993. Impacts of introduced predators on nesting seabirds in the northeast Pacific. Pages 218–226 *in* K. Vermeer, K.T. Briggs, K.H. Morgan, and D. Siegel-Causey (eds.), The status, ecology, and conservation of marine birds of the North Pacific. Special Publication, Canadian Wildlife Service, Ottawa, Ontario.

Banner, A.; Pojar, J.; Schwab, J.W.; Trowbridge, R. 1989. Vegetation and soils of the Queen Charlotte Islands: recent impacts of development. Pages 261–279 *in* G.G.E. Scudder and N. Gessler (eds.), The outer shores. Queen Charlotte Islands Museum Press, Skidegate, B.C.

Barker, J. 1998. Personal communication to T. Golumbia. Forester, Western Forest Products Ltd.

B.C. Game Commission. 1956. Letter from J. Hatter, Chief Game Biologist, to J. McLucus, dated 13 March 1956. British Columbia Archives.

B.C. Parks. 1992. Naikoon Park master plan background document (draft). Prepared for B.C. Parks, Ministry of Environment, Lands and Parks, March. 82 pp.

B.C. Parks. 1999a. Naikoon management plan. Prepared by B.C. Parks, Smithers, B.C., April. 112 pp.

B.C. Parks. 1999b. Naikoon Provincial Park cow assessment. Unpublished document prepared for B.C. Ministry of Environment, Lands and Parks, Skeena District. 10 pp.

Bennett, J. 1996. The effect of deer browsing on shrub and herbaceous plant growth and redcedar regeneration in Sewell Inlet, Queen Charlotte Islands. Report R8-5, F2421-20, Western Forest Products Ltd., Jordon River, B.C.

Bertram, D.F. 1989. The status of Ancient Murrelets breeding on Langara Island, British Columbia, in 1988. Technical Report Series No. 59, Canadian Wildlife Service, Pacific and Yukon Region, B.C.

Bertram, D.F. 1995. The role of introduced rats and commercial fishing in the decline of Ancient Murrelets on Langara Island, British Columbia. Conserv. Biol. 9(4): 865–872.

Bertram, D.F.; Nagorsen, D.W. 1995. Introduced rats, *Rattus* spp., in the Queen Charlotte Islands: Implications for seabird conservation. Can. Field-Nat. 109: 6–10.

Buck, P.E.F.; Henigman, J. 2000. Options to reduce deer browsing on Haida Gwaii/Queen Charlotte Islands. Final report to the South Moresby Forest Replacement Account Management Committee. 71 pp.

Burles, D. 2002. Personal communication to T. Golumbia, July. Gwaii Haanas staff.

Burles, D. 2004. Personal communication to T. Golumbia, September. Gwaii Haanas staff.

Burles, D.; Gardiner, D. 1991. Interim Park Conservation Plan for the proposed South Moresby/Gwaii Haanas National Park Reserve. Unpublished report for Parks Canada, Queen Charlotte City, B.C.

Burles, D.W.; Edie, A.G.; Bartier, P.M. 2004. Native land mammals and amphibians of Haida Gwaii: with management implications for Gwaii Haanas National Park Reserve and Haida Heritage Site. Technical Reports in Ecosystem Science No. 40, Parks Canada, Atlantic Region, Halifax, Nova Scotia. 119 pp.

Calder, J.A.; Taylor, R.L. 1968. Flora of the Queen Charlotte Islands. Part 1. Systematics of the vascular plants. Monograph No. 4, Research Branch, Department of Agriculture, Ottawa, Ontario. 659 pp.

Campbell, R.W.; Dawe, N.K.; McTaggart-Cowan, I.; Cooper, J.M.; Kaiser, G.W.; Stewart, A.C.; McNall, M.C.E. 1997. The birds of British Columbia. Vol. 3. Passerines. Flycatchers through vireos. Royal British Columbia Museum, Victoria, B.C., in association with the Canadian Wildlife Service. 693 pp.

Campbell, R.W.; Dawe, N.K.; McTaggart-Cowan, I.; Cooper, J.M.; Kaiser, G.W.; Stewart, A.C.; McNall, M.C.E. 2001. The birds of British Columbia. Vol. 4. Passerines. Wood-warblers through old world sparrows. Royal British Columbia Museum, Victoria, B.C., in association with the Canadian Wildlife Service. 739 pp.

Carl, G.C.; Guiguet, C.J. 1972. Alien animals in British Columbia. B.C. Provincial Museum Handbook 14, Victoria, B.C. 94 pp.

Carmichael, J. 2002. Personal communication; interviewed by K. Moore and T. Golumbia. Long-time resident of Queen Charlotte City, B.C.

Chittenden, H.H. 1884. Exploration of the Queen Charlotte Islands. Reprinted 1984. Gordon Soules Book Publishers, Vancouver, B.C. 93 pp.

Coates, K.D.; Pollack, J.C.; Barker, J.E. 1985. The effect of deer browsing on the early growth of three conifer species in the Queen Charlotte Islands. Research Report 85002-PR, B.C. Ministry of Forests, Victoria, B.C. 13 pp.

Cole, D.; Lockner, B. (eds.). 1993. To the Charlottes. George Dawson's 1878 survey of the Queen Charlotte Islands. University of British Columbia Press, Vancouver, B.C. 211 pp.

Collison, W.H. 1915. In the wake of the war canoe. Seeley, Sevice & Co., London, U.K. 352 pp.

Cook, F.S. 1947. Notes on some fall and winter birds of the Queen Charlotte Islands, British Columbia. Can. Field-Nat. 61(4): 131–133.

Dalzell, K.E. 1968. The Queen Charlotte Islands 1774–1966. Vol. 1. C.M. Adam, Terrace, B.C. 340 pp.

DeBucy, S. 1989. Personal communication; interviewed by K. Moore. Long-time resident of Queen Charlotte City, B.C.

DeBucy, S. 2001. Personal communication; interviewed by L. Bland. Long-time resident of Queen Charlotte City, B.C.

DeBucy, S. 2002. Personal communication; interviewed by K. Moore and T. Golumbia. Long-time resident of Queen Charlotte City, B.C.

Duff, W.; Kew, M. 1958. Anthony Island: A home of the Haidas. British Columbia Museum Report for 1957, Royal British Columbia Museum, Victoria, B.C.

Edie, A. 2000. Update COSEWIC status report on Queen Charlotte Islands ermine (*Mustela erminea haidarum* L.). Submitted to the Committee on the Status of Endangered Wildlife in Canada. 43 pp.

Emmott, F.N. 1918. Unpublished letter of 15 October 1918 to Provincial Game Warden W.G. McMynn. Provincial Game Warden's Correspondence, British Columbia Archives, Victoria, B.C.

Engelstoft, C.; Bland, L. 2002. Restoration priorities associated with introduced species impacts on Haida Gwaii/Queen Charlotte Islands: Perspectives and strategies. Report prepared for Council of the Haida Nation Forest Guardians and B.C. Ministry of Water, Land and Air Protection. 112 pp.

Fletcher, V. 1989. Personal communication with Keith Moore. Son of Game Commissioner J. Fletcher, Queen Charlotte City, B.C.

Foster, J.B. 1965. The evolution of the mammals of the Queen Charlotte Islands, British Columbia. B.C. Provincial Museum Occasional Paper 14, Victoria, B.C. 130 pp.

Foster, J.B. 1982. The Queen Charlotte Islands: The Canadian Galapagos. Unpublished report received by the Department of Botany, University of British Columbia, Vancouver, B.C., September. 11 pp.

Foster, J.B. 1989a. Conservation on the Queen Charlotte Islands. Pages 281–301 *in* G.G.E. Scudder and N. Gessler (eds.), The outer shores. Queen Charlotte Islands Museum Press, Skidegate, B.C.

Foster, J.B. 1989b. Personal communication; interviewed by K. Moore.

Gaston, A.J. 1994. Status of the Ancient Murrelet, *Synthliboramphus antiquus*, in Canada and the effects of introduced predators. Can. Field-Nat. 108: 211–222.

Gaston, A.J. 2003. Personal communication; interviewed by T. Golumbia.

Gaston, A.J.; Masselink, M. 1997. The impact of raccoons (*Procyon lotor*) on breeding seabirds at Englefield Bay, Haida Gwaii, Canada. Bird Conserv. Int. 7: 35–51.

Gill, R. 1999. Deer management to protect forest vegetation—a British perspective. Pages 59–68 *in* G.G. Wiggins (ed.), Proceedings of the cedar symposium: growing western redcedar and yellow-cypress on the Queen Charlotte Islands/Haida Gwaii. B.C. Ministry of Forests/Canada–British Columbia South Moresby Forest Replacement Account, Victoria, B.C.

Golumbia, T.E. 2000. Introduced species management in Haida Gwaii (Queen Charlotte Islands). Pages 327–331 *in* L.M. Darling (ed.), Proceedings of a conference on the biology and management of species and habitats at risk, Kamloops, B.C., 15–19 February 1999. Vol. 1. B.C. Ministry of Environment, Lands and Parks, Victoria, B.C., and University College of the Cariboo, Kamloops, B.C.

Golumbia, T. 2001. Gwaii Haanas terrestrial ecosystem conservation strategy. Unpublished report, Parks Canada, Queen Charlotte City, B.C. 149 pp.

Golumbia, T. 2002. St. James Island rat eradication program final report. Unpublished report, Parks Canada, Queen Charlotte City, B.C. 35 pp.

Gould, D. 1989. Personal communication; interviewed by K. Moore. Local resident, Sandspit, B.C.

Gray, J. 2001. Personal communication; interviewed by L. Bland. Biologist, Tlell, B.C.

Guiguet, C.J. 1946. Unpublished field notes, 11 May – 16 August 1946 and 6 May – 25 August 1947. British Columbia Archives.

Hagelund, W.A. 1987. Whalers no more. Harbour Publishing Co. Ltd., Madeira Park, B.C. 211 pp.

Hall, W. 1937. Moresby Forest: Survey and preliminary management plan. Unpublished report, B.C. Forest Service, Victoria, B.C.

Hamel, P.J.; Hearne, M. 2001. Checklist of the birds of the Queen Charlotte Islands/Haida Gwaii. Unpublished report submitted to Gwaii Haanas National Park Reserve, 27 March, Queen Charlotte City, B.C.

Harfenist, A. 1994. Effects of introduced rats on nesting seabirds of Haida Gwaii. Technical Report Series No. 218, Canadian Wildlife Service, Pacific and Yukon Region, B.C.

Harfenist, A.; MacDowell, K.; Golumbia, T.; Schultz, G. 2000. Monitoring and control of raccoons on seabird colonies in Haida Gwaii (Queen Charlotte Islands). Pages 333–339 *in* L.M. Darling (ed.), Proceedings of a conference on the biology and management of species and habitats at risk, Kamloops, B.C., 15–19 February 1999. Vol. 1. B.C. Ministry of nvironment, Lands and Parks, Victoria, B.C., and University College of the Cariboo, Kamloops, B.C.

Harrison, C. 1925. Ancient warriors of the North Pacific: the Haidas, their laws, customs and legends, with some historical account of the Queen Charlotte Islands. H.F. & G. Witherby, London, U.K. 222 pp.

Hartman, L.H. 1993. Ecology of coastal raccoons (*Procyon lotor*) on the Queen Charlotte Islands, British Columbia, and evaluation of their potential impact on native burrow-nesting seabirds. M.Sc. thesis, University of Victoria, Victoria, B.C.

Hartman, L.; Eastman, D. 1999. Distribution of introduced raccoons (*Procyon lotor*) on the Queen Charlotte Islands: Implications for burrow-nesting seabirds. Biol. Conserv. 88: 1–13.

Hartman, L.; Gaston, A.J.; Eastman, D. 1997. Raccoon predation on Ancient Murrelets on East Limestone Island, British Columbia. J. Wildl. Manage. 61: 377–388.

Henigman, J.; Martinz, M. 2000. Evaluation of deer browse barrier products to minimize mortality and growth loss to western redcedar. Unpublished report submitted to the Canada – British Columbia South Moresby Forest Replacement Account Management Committee. 49 pp.

Hilgemann, J. 2002. Personal communication with T. Golumbia, June.

Husband, G. 1989. Personal communication; interviewed by K. Moore. Long-time resident and local trapper, Tlell, B.C.

Husband, G. 2001. Personal communication; interviewed by L. Bland, June. Long-time resident and local trapper, Tlell, B.C.

IUCN (The World Conservation Union). 2001. Invasive Species Specialist Group web site: http://www.issg.org/index.html#Invasives.

Kaiser, G. 2001. Personal communication to T. Golumbia.

Kaiser, G.W.; Taylor, R.H.; Buck, P.D.; Elliott, J.E.; Howald, G.R.; Drever, M.C. 1997. The Langara Island Seabird Habitat Recovery Project: eradication of Norway rats—1993–1997. Technical Report Series No. 304, Canadian Wildlife Service, Pacific and Yukon Region, Delta, B.C. 81 pp.

Laskeek Bay Conservation Society. 1996. Newsletter No. 3. Queen Charlotte City, B.C. 12 pp.

Laskeek Bay Conservation Society. 1998. Natural connections—Newsletter of the Laskeek Bay Conservation Society. Queen Charlotte City, B.C., March. 6 pp.

Lee, L. 2001. Personal communication; interviewed by L. Bland. Biologist, Tlell, B.C.

Lemon, M. 1993. Survey of the Ancient Murrelet colony at Dodge Point, Lyell Island, in 1992. Pages 38–51 *in* A.J. Gaston (ed.), Laskeek Bay Conservation Society Science Report, 1992. Laskeek Bay Conservation Society, Queen Charlotte City, B.C.

Lewis, T. 1982. Ecosystems of tree farm license 24. Unpublished report prepared for Western Forest Products Ltd. 185 pp.

Lindsey, C.C. 1989. Part 2. Biotic characteristics of the Queen Charlotte Islands. Pages 107–108 *in* G.G.E. Scudder and N. Gessler (eds.), The outer shores. Queen Charlotte Islands Museum Press, Skidegate, B.C.

Lomer, F.; Douglas, G.W. 1999. Additions to the vascular plant flora of the Queen Charlotte Islands, British Columbia. Can. Field-Nat. 113: 235–240.

Madrone Consultants Ltd. 1992. Naikoon Provincial Park vegetation and biodiversity assessment. Prepared for B.C. Parks, Northern B.C. Region, October.

Marrs, C. 2001. Personal communication; interviewed by L. Bland. Fish habitat technician, Port Clements, B.C.

Martin, J.-L. 1995. Report on the results of field reconnaissance trip for study of introduced species impacts. Unpublished report to the Archipelago Management Board. 3 pp.

Martin, J.-L. 2003. Personal communication; interviewed by T. Golumbia.

Martin, J.-L.; Baltzinger, C. 2002. Interaction among deer browsing, hunting, and tree regeneration. Can. J. For. Res. 32: 1254–1264.

Martin, J.-L.; Joron, M. 2003. Nest predation in forest birds: influence of predator type and predator's habitat quality. Oikos 102: 641–653.

Martin, J.-L.; Joron, M.; Gaston, A.J. 2001. The squirrel connection: Influence of squirrels as songbird nest predators in Laskeek Bay. Pages 43–60 *in* A.J. Gaston (ed.), Laskeek Bay Research 10. Laskeek Bay Conservation Society, Queen Charlotte City, B.C.

Mathers, W. 1989. Personal communication; interviewed by K. Moore. Long-time resident of Sandspit, B.C.

McCrea, A.K. 1976. Westward wanderer: Synopsis of the life of "Andy" McCrea. Pages 55–57 *in* The Charlottes—A journal of the Queen Charlotte Islands. Vol. 4. The Queen Charlotte Islands Museum Society.

McTaggart-Cowan, I. 1989. Birds and mammals on the Queen Charlotte Islands. Pages 175–186 *in* G.G.E. Scudder and N. Gessler (eds.), The outer shores. Queen Charlotte Islands Museum Press, Skidegate, B.C.

Moore, K. 1988. Problem, issue, concern statement. Unpublished report prepared for Parks Canada, Queen Charlotte City, B.C. 7 pp.

Moore, K. 1992. Naikoon Park master plan background document. Unpublished report, B.C. Parks, Smithers, B.C. 82 pp.

Moore, K. 2001. Personal communication; interviewed by L. Bland. Queen Charlotte City, B.C.

Moors, P.J.; Atkinson, I.A.E. 1984. Predation on seabirds by introduced animals and factors affecting its severity. Pages 667–690 *in* J.P. Croxall, P.G.H. Evans, and R.W. Schreiber (eds.), Status and conservation of the world's seabirds. Technical Publication No. 2, International Council for Bird Preservation, Cambridge, U.K.

Osgood, W.H. 1901. Natural history of the Queen Charlotte Islands, British Columbia. North American Fauna No. 21, Government Printing Office, Washington, D.C. 87 pp.

Ovaska, K. 2002. Personal communication with T. Golumbia, 12 August.

Patch, C.A. 1922. A biological reconnaissance on Graham Island of the Queen Charlotte Group. Can. Field-Nat. 36: 100–105.

Phillips, H.B. 1956. Letter to Mr. B.J. Bacon, Fish and Game Council, Mainland North Coast Zone, Prince Rupert, B.C., dated 12 November. British Columbia Archives.

Piket, E. 1989. Personal communication; interviewed by K. Moore. Long-time resident of Queen Charlotte City, B.C.

Pojar, J.; Banner, A. 1984. Old growth forests and introduced black-tailed deer on the Queen Charlotte Islands, British Columbia. Pages 247–257 *in* W.R. Meehan, T.R. Merrell, Jr., and T.A. Hanley (eds.), Fish and wildlife relationships in old-growth forests: Proceedings of a symposium held in Juneau, Alaska, 12–15 April 1982. American Institute of Fishery Research Biologists, Morehead City, North Carolina.

Pojar, J.; Lewis, T.; Roemer, H.; Wilford, D.J. 1980. Relationships between introduced black-tailed deer and the plant life in the Queen Charlotte Islands, British Columbia. Unpublished report, B.C. Ministry of Forests, Smithers, B.C. 63 pp.

Poole, F. 1872. Queen Charlotte Islands: a narrative of discovery and adventure in the north Pacific. Hurst and Blackett, London, U.K.

Powell, D. 1988. Raccoon colonization of South Moresby Island, Queen Charlotte Islands. Unpublished report, Wildlife Branch, B.C. Ministry of Environment, Lands and Parks, Smithers, B.C. 14 pp.

Pritchard, A.L. 1934. Was the introduction of the muskrat to Graham Island, Queen Charlotte Islands, unwise? Can. Field-Nat. 48: 103.

Province of British Columbia. 1914. Annual report of the B.C. Game Commission. Victoria, B.C.

Province of British Columbia. 1918. Annual report of the B.C. Game Commission. Victoria, B.C.

Province of British Columbia. 1920. Annual report of the B.C. Game Commission. Victoria, B.C.

Province of British Columbia. 1925. Annual report of the B.C. Game Commission. Victoria, B.C.

Province of British Columbia. 1928. Annual report of the B.C. Game Commission. Victoria, B.C.

Province of British Columbia. 1929. Annual report of the B.C. Game Commission. Victoria, B.C.

Province of British Columbia. 1930. Annual report of the B.C. Game Commission. Victoria, B.C.

Province of British Columbia. 1936. Annual report of the B.C. Game Commission. Victoria, B.C.

Province of British Columbia. 1937. Annual report of the B.C. Game Commission. Victoria, B.C.

Province of British Columbia. 1938. Annual report of the B.C. Game Commission. Victoria, B.C.

Province of British Columbia. 1944. Annual report of the B.C. Game Commission. Victoria, B.C.

Province of British Columbia. 1948. Annual report of the B.C. Game Commission. Victoria, B.C.

Province of British Columbia. 1950. Annual report of the B.C. Game Commission. Victoria, B.C.

Province of British Columbia. 1951. Annual report of the B.C. Game Commission. Victoria, B.C.

Province of British Columbia. 1954. Annual report of the B.C. Game Commission. Victoria, B.C.

Province of British Columbia. 1955. Annual report of the B.C. Game Commission. Victoria, B.C.

Province of British Columbia. 1956. Annual report of the B.C. Game Commission. Victoria, B.C.

Province of British Columbia. 1998. Furbearer harvest statistics 1985–1997. B.C. Ministry of Water, Land and Air Protection, Smithers, B.C.

Province of British Columbia. 1999. Deer harvest statistics 1988–1998. B.C. Ministry of Water, Land and Air Protection, Smithers, B.C.

Reimchen, T.E. 1991. Introduction and dispersal of the Pacific tree frog, *Hyla regilla*, on the Queen Charlotte Islands, British Columbia. Can. Field-Nat. 105: 288–290.

Reimchen, T.E. 1992. Naikoon Provincial Park, Queen Charlotte Islands/Haida Gwaii biophysical data for freshwater habitats. Prepared for B.C. Ministry of Environment, Lands and Parks by Islands Ecological Research, Queen Charlotte City, B.C.

Reimchen, T.E. 1993. Aquatic inventory report for South Moresby National Park. Unpublished report for Parks Canada, Queen Charlotte City, B.C.

Rennie, D. 2001. Personal communication; interviewed by L. Bland, June. Local resident of Port Clements, B.C.

Richardson, D. 1989. Personal communication; interviewed by K. Moore. Long-time resident of Tlell, B.C.

Richardson, D. 2001. Personal communication; interviewed by L. Bland. Long-time resident of Tlell, B.C.

Roberts, F. 1989. Personal communication; interviewed by K. Moore. Long-time resident of Queen Charlotte City, B.C.

Robinson, D.J. 1957. Status of certain animals and birds of the Queen Charlotte Islands, March 15–22, 1957. Unpublished report, B.C. Game Department, Nanaimo, B.C.

Rodway, M.S.; Lemon, M.J.F.; Kaiser, G.W. 1988. Canadian Wildlife Service Seabird Inventory Report No. 1: East coast of Moresby Island. Technical Report Series No. 50, Canadian Wildlife Service, Pacific and Yukon Region, Delta, B.C.

Ross, E. 1989. Personal communication; interviewed by K. Moore. Long-time resident of Tlell, B.C.

Ross, E. 2002. Personal communication; interviewed by K. Moore and T. Golumbia. Long-time resident of Queen Charlotte City, B.C.

Spalding, D.J. 1992. The history of elk (*Cervus elaphus*) in British Columbia. Contributions to Natural Science No. 18, Royal British Columbia Museum, Victoria, B.C. 27 pp.

Sugden, L.G. 1949. Report on live trapping beaver (*Castor canadensis leucodontus*) on Vancouver Island and transplanting them on Graham Island of the Queen Charlotte group. June–July 1949. Unpublished report, B.C. Game Commission. 8 pp.

Summers, K.; Rodway, M. 1988. Raccoon–seabird interactions (with notes on rats and marten) on Moresby Island, Queen Charlottes: A problem analysis. Unpublished report prepared for Wildlife Branch, B.C. Ministry of Environment, Lands and Parks, Smithers, B.C. 62 pp.

Taylor, R.L. 1989. Vascular plants of the Queen Charlotte Islands. Pages 121–125 *in* G.G.E. Scudder and N. Gessler (eds.), The outer shores. Queen Charlotte Islands Museum Press, Skidegate, B.C.

Taylor, R.H.; Kaiser, G.W.; Drever, M.C. 2000. Eradication of Norway rats for recovery of seabird habitat on Langara Island, British Columbia. Restor. Ecol. 8(2): 151–160.

Trenholme, N.S.; Hatter, I.W. 1975. Queen Charlotte Islands elk study. Unpublished report, Wildlife Branch, B.C. Ministry of Environment, Smithers, B.C. 11 pp.

VandenBrink, M.N.M. 1992. Raccoon–seabird interactions on the Queen Charlotte Islands: assessing the risk. Report for the 1992 synoptic survey. Wildlife Branch, B.C. Ministry of Environment, Lands and Parks, Smithers, B.C.

Vigneault, L. 2001. Personal communication; interviewed by L. Bland. Tlell, B.C.

Vila, B.; Vourc'h, G.; Gillon, D.; Martin, J.-L.; Guibal, F. 2002. Is escaping deer browse just a matter of time in *Picea sitchensis*? A chemical and dendroecological approach. Trees–Struct. Funct. 16: 488–496.

Vila, B.; Guibal, F.; Torre, F.; Martin, J.-L. 2003. Growth change of young *Picea sitchensis* in response to deer browsing. For. Ecol. Manage. 180: 423–424.

Walker, C.J. 1956. Letter to Commanding Officer, B.C. Game Commission, Prince George, dated 18 December. British Columbia Archives.

Western Forest Products. 1988. Deer exclosure trials. Unpublished report, Western Forest Products Ltd., Port McNeil, B.C.

Young, Reverend C.J. 1927. A visit to the Queen Charlotte Islands. Auk 4(1): 38–43.

Changes in vegetation of Haida Gwaii in historical time

Jim Pojar

Abstract

The natural vegetation of Haida Gwaii (Queen Charlotte Islands, British Columbia) has changed dramatically since 1850. Three introductions/invasions have had the largest and most persistent impacts on the natural vegetation: postindustrial humans, extensive clearcut logging, and Sitka black-tailed deer *Odocoileus hemionus sitkensis*. Colonial-era and modern human settlement have most significantly resulted in clearings, roads, and the introduction of weedy plant species that now dominate the vegetation of many open, disturbed habitats. Industrial logging has led to more landslides and increased erosion and deposition and, consequently, to the development of much early successional vegetation. Extensive clearcutting has also converted large areas of old, structurally complex forest to young, simplified forest. Heavy browsing by introduced deer has further simplified and homogenized the forest vegetation, depleting the understory and retarding the regeneration of trees, especially western redcedar *Thuja plicata* and yellow-cedar *Chamaecyparis nootkatensis*. Deer browsing has also contributed to the decline of ecologically, geographically, and culturally significant plant species of forested and nonforested communities.

> Biotic invasions are altering the world's natural communities and their ecological character at an unprecedented rate. If we fail to implement effective strategies to curb the most damaging impacts of invaders, we risk impoverishing and homogenizing the very ecosystems on which we rely to sustain our agriculture, forestry, fisheries and other resources and to supply us with irreplaceable natural services. Given the current scale of invasions and our lack of effective policies to prevent or control them, biotic invasions have joined the ranks of atmospheric and land-use change as major agents of human-driven global change.
>
> —Mack et al. (2000)

1. Introduction

The flora of Haida Gwaii (Queen Charlotte Islands, British Columbia) is well-known, but the vegetation was little studied formally (i.e., systematically, with quantitative plots) until the late 1970s. European settlement started around 1860, with several flurries of homestaking and townsite development related to whaling, fishing and processing, mining, logging and sawmilling, and cattle ranching. These developments and settlements have remained rather small and local, but cumulatively have had a large "ecological footprint." Industrial logging also commenced in the early 1900s, intensified in the war years (1917–1918 and late 1930s and the 1940s), expanded and became increasingly mechanized in the 1950s and 1960s, peaked in the 1970s, and continues to the present, but at lower rates of harvesting. Sitka black-tailed deer *Odocoileus hemionus sitkensis* were introduced to the Islands in the early 1900s and, in the near absence of predation, greatly increased in numbers and overran the archipelago, browsing as they went. These three introductions/invasions (postindustrial humans, mechanized logging, and black-tailed deer) have had manifold and long-lasting impacts on the native vegetation of Haida Gwaii. The vegetation has changed dramatically over the past 100 years. Much of this recent change was unremarked or unrecorded. Hence the story must be reconstructed, from the few available historical observations, from modern (i.e., post-1970) observations and studies, and from ecological interpretation, retrospection, and extrapolation.

2. Introduced species of vascular plants

The issue of introduced species on Haida Gwaii, their impacts and what to do about them, was addressed in a review by Engelstoft and Bland (2002). Although there are well over 100 species of introduced vascular plants on Haida Gwaii, most of them have not yet made significant inroads on native vegetation. To successfully invade most Haida Gwaii ecosystems, a plant must be shade-tolerant. Most weeds are not, but they do well in open, disturbed habitats. No doubt many Islanders are familiar with the ruderal vegetation of roadsides, clearings, gravel pits, fields, and pastures, where many of the plants are introduced. Think of such familiar species as dandelion *Taraxacum officinale*, foxglove *Digitalis purpurea*, Himalayan blackberry *Rubus discolor*, sheep sorrel *Rumex acetosella*, curled dock *Rumex crispus*, Canada and bull thistles *Cirsium arvense* and *C. vulgare*, ribwort plantain *Plantago lanceolata*, black medic *Medicago lupulina*, English daisy *Bellis perennis*, sow-thistles *Sonchus arvensis* and *S. oleraceus*, oxeye daisy *Leucanthemum vulgare*, pineapple weed *Matricaria*

discoidea, orange-red king-devil *Hieracium aurantiacum*, hairy cat's-ear *Hypochaeris radicata*, common groundsel *Senecio vulgaris*, shepherd's purse *Capsella bursa-pastoris*, common starwort *Stellaria media*, and the grasses, redtop *Agrostis gigantea*, silver hairgrass *Aira caryophyllea*, common velvet-grass *Holcus lanatus*, timothy *Phleum pratense*, annual bluegrass *Poa annua*, and barren fescue *Vulpia bromoides*. The seeding of roadcuts and cleared rights-of-way with commercial grass–legume mixtures (consisting of nonnative species) has also contributed to the alien ruderal vegetation along hundreds of kilometres of roads. The logic apparently is that eventually these aliens will be overtopped and shaded-out by the native vegetation, at least on deactivated roads. This remains to be seen.

In my opinion, the most dangerous introduced plants are Scotch broom *Cytisus scoparius*, gorse *Ulex europaeus*, Canada thistle *Cirsium arvense*, marsh thistle *C. palustre*, and Japanese knotweed *Polygonum cuspidatum*. Broom has probably had the most effect on native vegetation to date, invading several beach communities at Tlell, including open spruce forest as well as stabilized dune habitats.

The introduced wall lettuce *Lactuca muralis* and English ivy *Hedera helix* are shade-tolerant exceptions to the ruderal rule. Both are so far infrequent and local on Haida Gwaii. However, they require monitoring, for both have been very successful in forests of southwestern British Columbia. It is difficult to predict which species will eventually cause trouble, but some are probably time bombs that could tick for decades before they explode (Sakai et al. 2001; Simberloff this volume). The potentially most dangerous species would be a shade-tolerant shrub or herb that is unpalatable to deer and has a good dispersal mechanism. Such an understory species could rapidly take over the deer-depleted and often nearly vacant understory strata of the forests of Haida Gwaii.

The vegetation of sand beaches also appears to have changed significantly in historical time. Although the sand beaches superficially do not appear to have been significantly altered by humans, they have experienced direct and indirect impacts from grazing and logging (see section 5.2), respectively. They are also open, naturally unstable habitats, susceptible to invasion. The introduced European beachgrass *Ammophila arenaria* has become the dominant ground cover at several beaches, in the semistabilized parts of the beaches immediately behind the driftwood zone. Such dominance changes the dynamics of the beach and can result in a decline in species that form scattered colonies in these active but partly stabilized areas (Seabloom and Wiedemann 1994). I suspect that species that have declined include the sand-loving beach carrot *Glehnia littoralis*, sand-verbena *Abronia latifolia*, bur sage *Ambrosia chamissonis*, beach tansy *Tanacetum huronense*, beach lupine *Lupinus littoralis*, beach peavine *Lathyrus littoralis*, beach morning glory *Calystegia soldanella*, and even big-headed sedge *Carex macrocephala* and dune bluegrass *Poa macrantha*. Introduced weeds—species such as dandelion, hairy cat's-ear, common groundsel, field buttercup *Ranunculus acris*, common chickweed *Cerastium vulgatum*, sheep sorrel, field brooklime *Veronica arvensis*, silver hairgrass, common velvet-grass—have invaded the transition zone next to the closed forest. Scotch broom has also invaded this zone, as well as the adjacent beach forest, and poses a serious threat to the natural beach vegetation, as well as to other plant communities farther inland, as it invades along roadsides.

3. Fire

Natural fires have historically played a minor role in the forest ecology of Haida Gwaii. Parminter (1983) reported that from 1940 to 1982, only four lightning-caused fires were recorded for the archipelago, and none exceeded 0.1 ha in size. The history of older lightning-caused fires is poorly known. Pearson (1968) found evidence of major fires that burned around 1715 and 1855. Harris and Farr (1974), in southeast Alaska, noted that although age class structure suggests that several extensive fires burned between 1650 and 1850, the bulk of the forests are (as on Haida Gwaii) uneven-aged and do not owe their origin to fire. This also appears to be the case for the central and northern mainland coast of British Columbia (Pojar et al. 1999; Dorner and Wong 2002).

There are several large areas of postindustrial, human-caused fires. Some, especially along the east coast, were probably related to land clearing by settlers. Others were probably escaped slash fires after 1940s and 1950s logging, including a large intense fire that burned nearly 5000 ha around Skidegate Lake. Dalzell (1973) reported that a large fire burned from Masset to the headwaters of the Tlell River in about 1840. It is unclear how that fire started, but the excellent second growth of western hemlock *Tsuga heterophylla*, western redcedar *Thuja plicata*, Sitka spruce *Picea sitchensis*, and shore pine *Pinus contorta* var. *contorta* constitutes a very different forest from the original old-growth redcedar–hemlock stands.

4. Insects and diseases

I assume that species of insects and disease fungi that affect vegetation have remained at essentially background levels since 1850—with some notable exceptions, including the recent blackheaded budworm *Acleris gloverana* epidemic in the now-extensive young forests of Graham and Moresby islands. Green spruce aphid *Elatobium abietinum* was first reported from Haida Gwaii in 1961 (Engelstoft and Bland 2002). Several outbreaks have occurred several times since then, resulting in defoliation and sometimes mortality of Sitka spruce, especially along the east coast of the Islands.

5. Impacts of logging

5.1 Forests

The most dramatic and immediately apparent changes in upland forests have resulted from logging, including early clearing, firewood cutting, hand-logging, and A-framing, but more significantly modern clearcutting. Logging has many serious environmental impacts—on hydrology, fish and wildlife populations, slope stability—and huge visual impacts as well. For the most part, however, the plant species composition of the forests of Haida Gwaii has not changed permanently or significantly (at the landscape scale) because of logging. After cutting, the forests quickly

regrew, the secondary succession involving mostly the same species that were already there in the old growth, but in rather different proportions. The few postlogging slash fires that were large and intense, dating back to the 1940s and 1950s, did not seem to result in anything different from the prevailing young, dense conifer stands that have occupied cutover lands. There are pioneering exceptions, like red alder *Alnus rubra* and salmonberry *Rubus spectabilis*. However, they typically establish after exposure of mineral soil or parent material or rock, as part of primary succession on bare surfaces (Smith et al. 1986).

No doubt the early mechanized logging, when creeks were used as skid roads and "nontimber forest resources" were a nonconcept, caused much erosion and initiation of seres dominated by red alder and deciduous shrubs. Conventional clearcut logging (which has prevailed on Haida Gwaii since about 1940) and especially the attendant road development can trigger landslides and exacerbate floods, and of course there is the network of roads. Mass wasting (landslides, debris flows and torrents, slump earth-flows, bedrock failures) and shifts in stream channels are dominant geomorphic processes on Haida Gwaii, especially in mountainous terrain—and will continue to be so (Clague 1989). The steep slopes of the Queen Charlotte Ranges and the Skidegate Plateau are inherently unstable, and logging such slopes (which often support terrific stands of trees) continues to cause problems, significantly accelerating rates of mass wasting and modifying fluvial structure and processes downstream (Hogan 1986; Banner et al. 1989). Otherwise, modern coastal logging usually does not provide a lot of exposed mineral substrates.

Forest regeneration and regrowth are mostly not a problem, except in the case of deer browsing and (especially) cedars. It would be virtually impossible to stop trees from growing on most of Haida Gwaii, and western hemlock will grow on most logged sites. Epixylic (growing on decaying wood) species of bryophytes do not seem to have suffered too much, again at the landscape scale. There are still lots of coarse woody debris (including big pieces) and a variety of microhabitats in the second-growth forest. That is largely because logging is still mostly of old forests, and much wood (so-called culls and slash) is left behind.

The major ecological impact of logging has been the enormous change, essentially a reversal, in the age class distribution of forests over the landscape. Large areas, tens of thousands of hectares, especially in the heavily timbered heart of the Skidegate Plateau, of what was over 90% old forest (250+ years, often 500+ years old) have been converted to 90% young forests (less than 50 years old). The young forests are still forests, but they are very different from old growth, structurally, functionally, and as habitat for other organisms (Lertzman et al. 1997; Carey 1998). Forests of all types and age classes are important for maintaining the diversity of all groups of organisms, from microbes to mammals. However, elements of biodiversity associated with old or late successional forests are very significant in the rainforest landscapes. Widespread conversion of old-growth forests to young production forests on a 60- to 80-year rotation has major impacts on the late successional elements. Some groups of organisms (e.g., specialist canopy invertebrates, epiphytic bryophytes and lichens, epixyles) are more sensitive to these impacts than are other generalist, vagile groups (e.g., most vertebrates). On Haida Gwaii, widespread industrial logging has not been going on long enough for these impacts to fully manifest themselves, nor have most of the impacts been studied or monitored. I would predict that the long-term consequences of conventional short-rotation forestry at the present rate of cut will be further impoverishment of native biota, accompanied by an increase in introduced and generalist native species.

5.2 Nonforested vegetation

Two maritime vegetation types have been indirectly but significantly altered by logging. Amount of driftwood is a major factor in the dynamics of beaches and their vegetation. No doubt beaches have always had driftwood, but amounts have increased significantly since the advent of industrial logging, with log booms, rafts, log drives on rivers, and increased levels of erosion along streams (see Maser et al. 1988). The driftwood armours the beaches, increasing the extent of the driftwood zone and evidently accreting to seaward, thus expanding the semistabilized area and the habitat available for colonizing plants—native and introduced.

Some tidal marshes, especially in sheltered inlets, have been damaged by logging-related activities, such as log booming and float camps, accompanied by fuel spills, and by deposition of bark and logs and gouging by logs. Subtidal communities such as beds of eelgrass *Zostera marina* have probably been most affected.

In both vegetation types, grazing by introduced cattle and deer has also facilitated the establishment of weedy species.

6. Impacts of introduced mammals, particularly deer

6.1 Historical observations

Geologist G.M. Dawson surveyed the Islands in 1878 and even collected plants. He was an outstanding field naturalist and astute observer, but unfortunately scarcely remarked (Cole and Lockner 1989) on understory vegetation in what were deer-free conditions. Most early explorers and scientifically oriented visitors such as F. Boas and C.F. Newcombe similarly recorded few observations about relative abundance or density of plants other than trees. Even Calder and Taylor (1968) generally made only passing mention of the impacts of deer, noting heavy grazing of maritime vegetation and the lack of any continuous understory shrub layer or ground cover of herbs in the upland forest. They did, however, observe that "the severe browsing of young seedlings of western red cedar by deer suppresses the development of the species in all regions we have studied."

Some early foresters recorded telling observations about the understory. In a timber cruise of western hemlock–Sitka spruce–western redcedar forests on northeastern Moresby Island, Gregg (1923) noted that "the underbrush is usually very dense, the principal species being salal

[*Gaultheria shallon*], huckleberry [*Vaccinium parvifolium*], and devil's club [*Oplopanax horridus*]."

Hopkinson (1931) remarked that "The luxuriant growth of vegetation in the Queen Charlotte Islands is most striking. The forests are a jungle and to traverse them it is necessary in many places to cut one's way through an undergrowth composed of such plants as red huckleberry [*Vaccinium parvifolium*], tall bilberry [*V. alaskaense*], thimbleberry [*Rubus parviflorus*], salmonberry, salal, and devil's club growing eight or ten feet in height....Beautiful ferns abound....Another noteworthy plant growing in the muskeg country, with leaves three and four feet long, is the skunk cabbage [*Lysichiton americanum*]...."

Another timber surveyor (Hall 1937) noted that "the only major deterrents to natural regeneration appear to be dense slash, salal, and berry bushes. The salal attains ten feet in height and forms an unbroken cover." Hall found 2-m-high salmonberry mixed with salal and devil's-club on moister sites, such as poorly drained slopes and creek bottoms, and devil's-club growing to 3 m in height and forming a solid cover in creek bottoms. Moreover, he maintained that immature forests "all contain hemlock, spruce and cedar in varying proportions" but there was "a preponderance of cedar in the younger stands."

By the 1950s, wildlife biologists were also noticing impacts. McTaggart-Cowan (1951) recorded the observations of local residents that there used to be heavy undergrowth of salmonberry along the lower Tlell River, lower Gold Creek used to be bordered with salal, and "skunk cabbage was abundant at one time but has been eliminated." Robinson (1957) observed that "The slashes which have been burnt look like Vancouver Island burns with one exception, this is the large amount of grass growing. There is a noticeable absence of deciduous and shrub species, whether this is influenced by deer is unknown. *Vaccinium* spp. and red cedar in the burnt slashes are browsed heavily and arouse the suspicions that deer are influencing the plant association."

The picture that emerges from these accounts is of an increasing impact of deer on vegetation, but an impact that, even in the 1960s and early 1970s, was not yet perceived as drastic or severe, except perhaps in the case of redcedar.

6.2 Recent (modern) observations

Forest ecologists began extensive sampling of vegetation and soils on Haida Gwaii in the late 1970s. They soon concluded that browsing by introduced deer had greatly modified the vegetation of the islands (Pojar et al. 1980; Pojar and Banner 1984; Banner et al. 1989; Pojar 1999). Their conclusions have been corroborated by the recent work of J.-L. Martin and collaborators and the Laskeek Bay Conservation Society (e.g., Daufresne and Martin 1997; Martin and Daufresne 1999; Engelstoft 2001; Vila et al. 2001; Engelstoft this volume; Stockton this volume).

6.2.1 Upland forest

Overbrowsing by introduced deer has apparently altered the structure of the forest vegetation and has virtually eliminated or greatly reduced preferred forage species in many areas (Pojar et al. 1980; Pojar and Banner 1984; Pojar 1999). Deer browsing has seriously depleted and sometimes eliminated western redcedar as regeneration in many old forests as well as on logged-over sites (Bennett 1996; Martin and Baltzinger 2002). Yellow-cedar has also suffered, especially in montane forests, but has not been as severely reduced overall as redcedar. Deer have affected Sitka spruce much less, but locally have eaten it back heavily (Vila et al. 2001; Vila and Martin this volume). Browsing has affected western hemlock least overall.

There has been a dramatic reduction in the shrub and herb layers of most of the forests of Haida Gwaii. Deer have heavily browsed huckleberry and blueberry [*Vaccinium* spp.], false azalea *Menziesia ferruginea*, salal, and salmonberry, among other shrubs. The near-removal of the shrub layer is particularly significant (Stockton this volume). The northwestern temperate rainforest is fundamentally a conifer–ericaceous shrub–moss system (Pojar et al. 1997) in which mycorrhizae (including ericaceae-type mycorrhizae) play key nutritional roles. In addition to the obvious structural change, the elimination of the ericaceous shrubs and their mycorrhizae could have major functional consequences in these forests.

Deer have also depleted ferns (lady fern *Athyrium filix-femina*, spiny wood fern *Dryopteris assimilis*, oak fern *Gymnocarpium dryopteris*, deer fern *Blechnum spicant*, and sword fern *Polystichum munitum*), as well as other typical coastal forbs, such as twisted-stalks *Streptopus amplexifolius* and *S. lanceolatus*, bunchberry *Cornus canadensis*, and five-leaved bramble *Rubus pedatus*. Table 1 summarizes the apparent impact of browsing on Haida Gwaii on zonal or "average" old-growth forests.

The suggestion that deer could have a destabilizing effect on steep slopes, due to the removal of shrubs and subsequent decay and nonreplacement of their roots (Pojar et al. 1980), was criticized by some as a diversionary tactic to draw attention away from the effects of clearcut logging. Nevertheless, I believe that this destabilization has indeed

Table 1
Prominence value (mean cover × square root of frequency) of typical shrubs and herbs in 20 × 20 m plots in zonal forests of Haida Gwaii and the northern coastal mainland of British Columbia

Species	Haida Gwaii $n = 69$	Northern mainland coast $n = 48$
Shrubs		
Red huckleberry *Vaccinium parvifolium*	25	33
Alaska blueberry *Vaccinium alaskaense*	20	330
Oval-leaved blueberry *Vaccinium ovalifolium*	5	62
False azalea *Menziesia ferruginea*	7	46
Herbs		
Deer fern *Blechnum spicant*	18	38
Spiny wood fern *Dryopteris assimilis*	2	26
Rosy twisted-stalk *Streptopus lanceolatus*	2	32
Clasping-leaved twisted-stalk *Streptopus amplexifolius*	2	8
Bunchberry *Cornus canadensis*	1	36
Five-leaved bramble *Rubus pedatus*	1	53

occurred. Even in intact old-growth forest on steep slopes, small-scale mass wasting is frequent (see also Johnson and Wilcock 1998). The bryophyte response to this appears to be an increase in mosses of mineral substrates and recently disturbed surfaces (species of the haircap moss group—*Pogonatum*, *Polytrichum*, and *Atrichum*, most noticeably), at the expense of weft-formers like lanky moss *Rhytidiadelphus loreus* and step moss *Hylocomium splendens*. The weft-formers are the dominant species of the thick moss carpets of undisturbed forest floors in old growth.

Effects of browsing on understory vegetation are especially noticeable in richer, more productive seepage and alluvial sites, as well as in zonal forests. Table 2 shows the apparent impact of browsing on typical shrubs and herbs in old-growth floodplain forests on Haida Gwaii. Compared with the mainland coast, note the major decreases in abundance for salmonberry, devil's-club, lady fern, oak fern, and skunk cabbage and the major increase in grass cover. At present, there are dramatic differences in understory between old-growth forests of Haida Gwaii and comparable forests on the northern B.C. mainland and on northern Vancouver Island.

These and similar data and observations from the thousands of relevés (sample plots) done over the past 30 years in the coastal forests of British Columbia provide strong circumstantial evidence that the forests of Haida Gwaii have changed significantly in the last 100 years, and much of the change (at least in understory vegetation) is due to deer browsing.

Table 2
Prominence value (mean cover × square root of frequency) of typical shrubs and herbs in 20 × 20 m plots in alluvial Sitka spruce forests of Haida Gwaii and the northern coastal mainland of British Columbia

Species	Haida Gwaii $n = 15$	Northern mainland coast $n = 12$
Shrubs		
Devil's-club *Oplopanax horridus*	2	260
Salmonberry *Rubus spectabilis*	3	109
Alaska blueberry *Vaccinium alaskaense*	4	74
Oval-leaved blueberry *Vaccinium ovalifolium*	11	33
Stink currant *Ribes bracteosum*	1	42
Herbs		
Foamflower *Tiarella trifoliata*	5	69
Rosy twisted-stalk *Streptopus lanceolatus*	4	91
Clasping-leaved twisted-stalk *Streptopus amplexifolius*	2	8
False lily-of-the-valley *Maianthemum dilatatum*	4	35
Bunchberry *Cornus canadensis*	1	69
Skunk cabbage *Lysichiton americanus*	1	31
Five-leaved bramble *Rubus pedatus*	1	69
Tall trisetum *Trisetum canescens*	36	1
Other grasses[a]	117	–
Oak fern *Gymnocarpium dryopteris*	25	95
Deer fern *Blechnum spicant*	4	16
Lady fern *Athyrium filix-femina*	9	43
Spiny wood fern *Dryopteris assimilis*	4	25

[a] Hairy wildrye *Elymus hirsutus*, Alaska oniongrass *Melica subulata*, bearded fescue *Festuca subulata*, Nootka reedgrass *Calamagrostis nutkaensis*.

6.2.2 Maritime vegetation

Shoreline plant communities have been subjected to very heavy browsing by deer, probably because the deer are forced to tidewater in tough snowy winters, and also because there can be a fair amount of forage in these habitats. As elsewhere, the deer concentrate on shrubs (*Vaccinium* spp., salal, thimbleberry *Rubus parviflorus*, salmonberry, Scouler's willow *Salix scouleriana*, snowberry *Symphoricarpos albus*, black twinberry *Lonicera involucrata*, and Pacific crab apple *Malus fusca*), young trees (even young Sitka spruce and western hemlock), ferns, and forbs—particularly those in the lily family. Consequently, shoreline vegetation has been greatly modified. Especially noticeable is the lack of showy flowered herbs in spring on rocky shorelines, where once had been displays of black lily *Fritillaria camschatcensis*, hairy cinquefoil *Potentilla villosa*, sea blush *Plectritis congesta*, monkey flower *Mimulus guttatus*, Siberian miner's lettuce *Claytonia sibirica*, pretty shooting star *Dodecatheon pulchellum*, western rattlesnake-root *Prenanthes alata*, red columbine *Aquilegia formosa*, western buttercup *Ranunculus occidentalis*, false lily-of-the-valley, round-leaved harebell *Campanula rotundifolia*, Alaska paintbrush *Castilleja unalaschcensis*, and Nootka lupine *Lupinus nootkatensis*, among others (see Stockton this volume). As native species have declined, introduced species have significantly increased in these habitats, especially near settlements and along roads. The invaders include several grasses (silver and early hairgrass, soft brome *Bromus hordeaceus*, sweet vernalgrass *Anthoxanthum odoratum*, common velvet-grass) and numerous forbs, such as common chickweed, hairy cat's-ear, English daisy, common sow-thistle *Sonchus oleraceus*, ribwort plantain, field buttercup, sheep sorrel, and white clover *Trifolium repens*.

Deer and, in places, cattle heavily graze tidal marshes, but the tidelands do not seem to have been as severely impacted as upland communities, probably because most of the species have underground rhizomes and are adapted to grazing by bears, geese, and deer.

6.2.3 Wetland vegetation

Freshwater wetlands are among the most conspicuous ecosystems on Haida Gwaii. Introduced beaver have modified some wetlands, most noticeably on the Graham Island lowlands, where beaver were first introduced. Some swamps have been flooded, as has some adjacent forestland. Typically the flooding kills the trees, and the wetland gradually becomes shallow open water or eventually a fen or marsh. Beavers reportedly have been killing the Pacific crab apple that fringes some open wetlands, as at Mayer Lake. Deer browsing has greatly reduced such characteristic swamp and bog forest species as skunk cabbage, salmonberry, deer fern, and other ferns, as well as young redcedar and yellow-cedar. Skunk cabbage, a robust understory plant in most coastal swamps in British Columbia, is especially noticeable by its absence or woeful puniness.

6.2.4 High-elevation vegetation

Deer browsing appears to have had less impact at high elevations, but the impact seems to be increasing or becoming more evident over the 25 years we have been watching. This is a major threat to rare and endemic species of vascular plants, the majority of which are species restricted to, or most abundant at, high elevations. Subalpine and alpine hotspots of vascular plant diversity occur, as at Takakia Lake and around Mount La Pérouse and Mount de la Touche. The impact of the apparently introduced mountain goats *Oreamnos americanus* on the high-elevation vegetation and rare/endemic plant taxa of Olympic National Park in Washington State provides a cautionary, albeit somewhat equivocal, tale (Lyman 1994; Hutchins 1995).

More than 20 years ago, we speculated that "Some rare vascular plant species on the Charlottes will become even rarer. Others, including most of the uncommon species of the mountains, are not immediately threatened by deer because of their preference for rocky high-elevation steeplands. However, given time and an increasingly desperate herbivore, some of these species could become restricted to the most inaccessible microhabitats" (Pojar et al. 1980). Subsequently, R.T. Ogilvie noted that "Twelve years later, these implications have been confirmed. The excessive deer populations are the most serious threat to the endemic and rare flora of the Queen Charlotte Islands" (Ogilvie 1994).

Conceivably, climate change could result in a decline in alplands, as timberline moves upward and pinches off the alpine sky islands—unless Haida Gwaii becomes more like the Aleutian Islands, with a hypermaritime tundra even at low elevations.

7. Conclusions

Three introductions/invasions—postindustrial humans, extensive clearcut logging, and black-tailed deer—have had manifold, serious, and long-lasting impacts on the natural vegetation of Haida Gwaii.

Post-1850 human settlement has had many direct and indirect effects, but the persistent, ecosystem-level impacts on vegetation relate primarily to clearings, roads, and the introduction of weedy species that have come to dominate the ruderal vegetation of open, disturbed habitats. Industrial logging has resulted in increased rates of mass wasting and changes to stream channel morphology, with subsequent development of early successional vegetation. Extensive clearcutting has also greatly altered the age class distribution of stands of trees over many forested landscapes, with large areas now covered by young forest with a simplified understory, structure, and epiphytic component. Heavy browsing by introduced deer has drastically depleted the shrub and herb layers of forests; has retarded regeneration of trees, especially western redcedar and yellow-cedar; and is contributing to the population declines of the cedars and of endemic and geographically significant plant species.

Literature cited

Banner, A.; Pojar, J.; Schwab, J.W.; Trowbridge, R. 1989. Vegetation and soils of the Queen Charlotte Islands: recent impacts of development. Pages 261–279 *in* G.G.E. Scudder and N. Gessler (eds.), The outer shores. Queen Charlotte Islands Museum Press, Skidegate, B.C.

Bennett, J. 1996. The effect of deer browsing on shrub and herbaceous plant growth and redcedar regeneration in Sewell Inlet, Queen Charlotte Islands. Report R8-5, F2421-20, Western Forest Products Ltd., Vancouver, B.C.

Calder, J.A.; Taylor, R.L. 1968. Flora of the Queen Charlotte Islands. Part 1. Systematics of the vascular plants. Monograph 4, Research Branch, Department of Agriculture, Ottawa, Ontario. 659 pp.

Carey, A.B. 1998. Ecological foundations of biodiversity: lessons from natural and managed forests of the Pacific Northwest. Northwest Sci. 72: 127–133.

Clague, J.J. 1989. Quaternary geology of the Queen Charlotte Islands. Pages 65–74 *in* G.G.E. Scudder and N. Gessler (eds.), The outer shores. Queen Charlotte Islands Museum Press, Skidegate, B.C.

Cole, D.; Lockner, B. 1989. The journals of George M. Dawson: British Columbia, 1875–1878. Vols. 1 and 2. University of British Columbia Press, Vancouver, B.C.

Dalzell, K.E. 1973. The Queen Charlotte Islands. Book 2: Of places and names. Cove Press, Prince Rupert, B.C.

Daufresne, T.; Martin, J.-L. 1997. Changes in vegetation structure and diversity as a result of browsing by a large herbivore: the impact of introduced black-tailed deer in the primary forest of Haida Gwaii, B.C. Pages 2–27 *in* A.J. Gaston (ed.), Laskeek Bay Research 7. Laskeek Bay Conservation Society, Queen Charlotte City, B.C.

Dorner, B.; Wong, C. 2002. Natural disturbance dynamics on the north coast. Unpublished report, B.C. Ministry of Sustainable Resource Management, Smithers, B.C. 49 pp.

Engelstoft, C. 2001. Effects of Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) on understory in old-growth forests on Haida Gwaii (Queen Charlotte Islands), British Columbia. M.Sc. thesis, University of Victoria, Victoria, B.C. 113 pp.

Engelstoft, C.; Bland, L. 2002. Restoration priorities associated with introduced species impacts on Haida Gwaii/Queen Charlotte Islands: perspectives and strategies. Unpublished report, Council of the Haida Nation Forest Guardians/B.C. Ministry of Water, Land and Air Protection, Victoria, B.C. 111 pp.

Gregg, E.E. 1923. Cruise on Queen Charlotte Islands. Unpublished report, B.C. Forest Service, Victoria, B.C.

Hall, W. 1937. Moresby Forest: Survey and preliminary management plan. Survey No. R. 49, B.C. Forest Service, Victoria, B.C.

Harris, A.S.; Farr, W.A. 1974. The forest ecosystem of southeast Alaska. 7. Forest ecology and timber management. General Technical Report PNW-25, Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture, Portland, Oregon. 109 pp.

Hogan, D.L. 1986. Channel morphology of unlogged, logged, and debris torrented streams in the Queen Charlotte Islands. Land Management Report No. 49, B.C. Ministry of Forests, Victoria, B.C. 94 pp.

Hopkinson, A.D. 1931. A visit to the Queen Charlotte Islands. Empire For. 10: 20–36.

Hutchins, M. 1995. Olympic mountain goat controversy continues. Conserv. Biol. 9: 1324–1326.

Johnson, A.C.; Wilcock, P. 1998. Effect of root strength and soil saturation on hillslope stability in forests with natural cedar decline in headwater regions of southeast Alaska. Pages 381–387 *in* M.J. Haigh, J. Krecek, G.S. Rajwar, and M.P. Kilmartin (eds.), Headwaters: water resources and soil conservation. A.A. Balkema, Rotterdam.

Lertzman, K.; Spies, T.; Swanson, F. 1997. From ecosystem dynamics to ecosystem management. Pages 361–382 *in* P.K. Schoonmaker, B. von Hagen, and E.C. Wolf (eds.), The rainforests of home: profile of a North American bioregion. Island Press, Washington, D.C.

Lyman, R.L. 1994. The Olympic mountain goat controversy: a different perspective. Conserv. Biol. 8: 898–901.

Mack, R.N.; Simberloff, D.; Lonsdale, W.M.; Evans, H.; Cout, M.; Bazzaz, F. 2000. Biotic invasions: causes, epidemiology, global consequences and control. Issues in Ecology No. 5, Ecological Society of America, Washington, D.C. 20 pp.

Martin, J.-L.; Baltzinger, C. 2002. Interaction among deer browsing, hunting, and tree regeneration. Can. J. For. Res. 32: 1254–1264.

Martin, J.-L.; Daufresne, T. 1999. Introduced species and their impacts on the forest ecosystem of Haida Gwaii. Pages 69–85 *in* G.G. Wiggins (ed.), Proceedings of the cedar symposium: growing western redcedar and yellow-cypress on the Queen Charlotte Islands/Haida Gwaii. B.C. Ministry of Forests/ Canada–British Columbia South Moresby Forest Replacement Account, Victoria, B.C.

Maser, C.; Tarrant, R.F.; Trappe, J.M.; Franklin, J.F. (eds.). 1988. From the forest to the sea: a story of fallen trees. General Technical Report PNW-GTR-229, Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture, Portland, Oregon.

McTaggart-Cowan, I. 1951. Report on the deer population of Graham Island, Q.C.I. Unpublished report, B.C. Game Department, Victoria, B.C.

Ogilvie, R.T. 1994. Rare and endemic vascular plants of Gwaii Haanas (South Moresby) Park, Queen Charlotte Islands, British Columbia. FRDA Report 214, Canada–British Columbia Partnership Agreement on Forest Resource Development, Victoria, B.C.

Parminter, J. 1983. Fire history and fire ecology in the Prince Rupert Forest Region. Pages 1–35 *in* R.L. Trowbridge and A. Macadam (eds.), Prescribed fire-forest soils, proceedings of a symposium. Land Management Report No. 16, B.C. Ministry of Forests, Victoria, B.C.

Pearson, W.J. 1968. A review and analysis of the fire history of the Queen Charlotte Islands. Unpublished report submitted to Association of British Columbia Professional Foresters, Vancouver, B.C. 49 pp.

Pojar, J. 1999. The effects of deer browsing on the plant life of Haida Gwaii. Pages 90–98 *in* G.G. Wiggins (ed.), Proceedings of the cedar symposium: growing western redcedar and yellow-cypress on the Queen Charlotte Islands/Haida Gwaii. B.C. Ministry of Forests/Canada–British Columbia South Moresby Forest Replacement Account, Victoria, B.C.

Pojar, J.; Banner, A. 1984. Old-growth forests and introduced black-tailed deer on the Queen Charlotte Islands, British Columbia. Pages 247–257 *in* W.R. Meehan, T.R. Merrell, Jr., and T.A. Hanley (eds.), Fish and wildlife relationships in old-growth forests. Proceedings of a symposium, 12–15 April 1982, Juneau, Alaska. American Institute of Fishery Research Biologists, Bethesda, Maryland. 425 pp.

Pojar, J.; Lewis, T.; Roemer, H.; Wilford, D.J. 1980. Relationships between introduced black-tailed deer and the plant life of the Queen Charlotte Islands, British Columbia. Unpublished report, B.C. Ministry of Forests, Smithers, B.C. 63 pp.

Pojar, J.; Klinka, K.; Meidinger, D.V.; Krestov, P.; Britton, G. 1997. Ericaceae (especially *Vaccinium*) in the forests of British Columbia: convergence, divergence, disturbance. Paper presented at the 40th annual symposium of the International Association of Vegetation Science, 18–22 August, Ceske Budejovice, Czech Republic.

Pojar, J.; Rowan, C.; MacKinnon, A.; Coates, D.; LePage, P. 1999. Silvicultural options in the Central Coast. B.C. Environment and Land Use Committee, Victoria, B.C. 97 pp.

Robinson, D.J. 1957. Status of certain animals and birds of the Queen Charlotte Islands, March 15–22, 1957. Unpublished report, B.C. Game Department, Nanaimo, B.C.

Sakai, A.K.; Allendorf, F.W.; Holt, J.S.; Lodge, D.M.; Molofsky, J.; With, K.A.; Baughman, S.; Cabin, R.J.; Cohen, J.E.; Ellstrand, N.C.; McCauley, D.E.; O'Neil, P.; Parker, I.M.; Thompson, J.N.; Weller, S.G. 2001. The population biology of invasive species. Annu. Rev. Ecol. Syst. 32: 305–332.

Seabloom, E.W.; Wiedemann, A.M. 1994. Distribution and effects of *Ammophila breviligulata* Fern. (American beachgrass) on the foredunes of the Washington coast. J. Coastal Res. 10: 178–188.

Smith, R.B.; Commandeur, P.R.; Ryan, M.W. 1986. Soils, vegetation, and forest growth on landslides and surrounding logged and old-growth areas on the Queen Charlotte Islands. Land Management Report No. 41, B.C. Ministry of Forests, Victoria, B.C. 95 pp.

Vila, B.; Guibal, F.; Martin, J.-L. 2001. Impact of browsing on forest in Haida Gwaii: a dendro-ecological approach. Pages 62–73 *in* A.J. Gaston (ed.), Laskeek Bay Research 10. Laskeek Bay Conservation Society, Queen Charlotte City, B.C.

Ecology of black-tailed deer in north coastal environments

Michael P. Gillingham

Abstract

This paper provides an overview of the ecology of black-tailed deer in different environments, with specific reference to their introduction to Haida Gwaii (Queen Charlotte Islands, British Columbia) and aspects of the ecology of Sitka black-tailed deer *Odocoileus hemionus sitkensis* that help us understand the impacts that black-tailed deer have had on Haida Gwaii; it emphasizes the flexibility of black-tailed deer in different environments. After reviewing the taxonomy of the *Odocoileus hemionus* subspecies found in British Columbia, I briefly examine the current population status and factors that influence local populations of black-tailed deer, including demographics, predation, the importance of cover and habitat, movements, and ecology. Coastal black-tailed deer are energy-limited, and their dietary and physiological flexibility are key to their success in coastal rainforests. Deer can take advantage of a large number of plant species, seasonal shifts in available species, and a variety of accessible habitats. Deer utilize high-quality food in summer to regain body mass, which is then depleted during winter, when food intake is less than energy requirements. The highest energetic costs to female deer are associated with late pregnancy and lactation, and these activities normally coincide with an abundance of new plant growth in spring. Sitka black-tailed deer impact their environment by removing large amounts of plant material during a growing season and woody material during winter. Over the long term, removal of fruiting or storage parts of plants can affect survival of the plants and, if sustained, the diversity of the forest. Overall, browsing impacts are influenced by the number and density of deer on the landscape and the ability of plants to defend themselves against and recover from browsing by deer.

1. Introduction

Sitka black-tailed deer *Odocoileus hemionus sitkensis* are an important species within the north coastal forests of British Columbia and southeast Alaska with respect to biological conservation, economic development, and human culture (Hanley 1993). Consequently, much has been written about this species, including both biological (e.g., McTaggart-Cowan 1945; Klein 1965; Wallmo and Schoen 1979; Schoen et al. 1981; Wallmo 1981a; Hanley 1984; Parker et al. 1999) and human (e.g., Nelson 1997) perspectives. Reviews of the ecology and management of Columbian black-tailed deer *Odocoileus hemionus columbianus* are even more extensive (e.g., Bunnell et al. 1978; Wallmo 1981a; Nyberg et al. 1989; Kie et al. 2002). It is impossible, therefore, to review the ecology of deer in north coastal environments in a brief and inclusive way. Instead, I focus on those aspects of Sitka black-tailed deer ecology (in relation to other black-tailed deer species) that demonstrate the flexibility of this species in a range of environments; an understanding of this flexibility should help us understand the impacts that black-tailed deer have had on Haida Gwaii since their introduction to the archipelago, a focus of this volume.

I begin with a summary of the taxonomy and distribution of the subspecies of deer found on Haida Gwaii (Queen Charlotte Islands, British Columbia) and the north coast of British Columbia and southeast Alaska. I then examine the key factors that affect their population dynamics, starting with demographics and population regulation with and without predators. Relying heavily on data collected for Sitka black-tailed deer over a continuous 2.5-year period (see Parker et al. 1993, 1996, 1999; Gillingham et al. 1997), I review nutrition and food habits and emphasize some of the interactions between these deer and their environment that should help us understand their success since being introduced to Haida Gwaii.

2. Taxonomy and range

As a species, mule deer *Odocoileus hemionus* are widespread and adaptable. The subspecies of mule deer inhabit a range of habitats, from the wet coastal forests of Alaska and British Columbia to dry desert environments and from the boreal forest of Yukon south to the interior semidesert shrub woodlands of northern Mexico (see Wallmo 1981b for a detailed review). Depending on the emphasis placed on overlap among subspecies, between 7 and 13 subspecies of mule deer have been recognized by taxonomists (e.g., McTaggart-Cowan 1956; Wallmo 1981b). More recently, Krausmann (1994) recognized 10 subspecies of *Odocoileus hemionus*, ranging from Alaska south to central Mexico.

Within British Columbia, there are three subspecies of mule deer. Although there are areas where

the distributions of the subspecies overlap (see Shackleton 1999), Rocky Mountain mule deer *Odocoileus hemionus hemionus* are generally found to the east of the coastal range and throughout much of the interior of the province, where they tend to prefer open forested areas or parklands with adjacent grasslands (Shackleton 1999). Along the coast, two other subspecies use the dense coastal rainforests as well as more open habitats, such as riparian and early successional stages of forests; the dense forest canopies afford a number of advantages to both Columbian black-tailed deer and Sitka black-tailed deer. These two subspecies are difficult to distinguish in the field, especially in areas where their ranges overlap. Columbian black-tailed deer are found across Vancouver Island (Shackleton 1999), on most of the smaller islands, and on the west slopes of the Coast Mountains north towards Rivers Inlet, where they begin to intergrade with the more northern Sitka black-tailed deer. The latter are found north of Rivers Inlet to the Portland Canal, where the distribution becomes patchy (Shackleton 1999). As discussed extensively throughout this volume, Sitka black-tailed deer were introduced several times onto some of the islands of Haida Gwaii beginning in the 1870s to provide venison for the local community. They are now very abundant on most of the larger islands in this archipelago, and they have colonized all but the smallest and most isolated offshore islands (Martin and Daufresne 1999). Throughout this review, I use the common name mule deer to refer specifically to work done on *O. h. hemionus*. In those instances where I refer generically to black-tailed deer, I am referring to both Columbian (*O. h. columbianus*) and Sitka (*O. h. sitkensis*) black-tailed deer, as in Wallmo (1981a).

3. Population status

In recent years, both mule deer and black-tailed deer populations have declined in many areas of the western United States and Canada; predation has been proposed frequently as a possible explanation (see review of Ballard et al. 2001). The effects of predator–prey relationships, however, are confounded by habitat carrying capacity, weather, human use patterns, and habitat alterations (Ballard et al. 2001). Consistent with the larger pattern of decline, black-tailed deer on Vancouver Island have been declining over the last two decades (B.C. Ministry of Environment, Lands, and Parks 2001). During the severe winter of 1968–1969 on Vancouver Island in particular, as many as 100 000 deer died of starvation.

Population estimates for coastal deer populations in British Columbia are approximate. For example, Sharpe (1999) indicated that no quantitative data for Sitka black-tailed deer populations on Haida Gwaii existed, because of the difficulty in counting this species. Nonetheless, estimates from 1997 contained in Shackleton (1999) suggest that there may be in excess of 65 000 Sitka black-tailed deer in British Columbia (inclusive of Haida Gwaii and mainland populations). Martin and Baltzinger (2002), however, speculate that there might be over 113 000 deer on Haida Gwaii. Other reports suggest that although mule and black-tailed deer populations are currently declining in 31% of their historic range (predominantly on Vancouver Island; B.C. Ministry of Environment, Lands, and Parks 2001), the Sitka black-tailed deer populations of coastal British Columbia and of Haida Gwaii are "stable" (B.C. Ministry of Environment, Lands, and Parks 2001).

4. Population demographics and regulation

As with most deer species, Sitka black-tailed deer populations can increase rapidly in number. Females usually do not breed until their second year, although first-year breeding has been observed (e.g., McCullough 1997; K.L. Parker and M.P. Gillingham, unpubl. data). After the first reproduction, females usually produce annually throughout an approximate life span of 10 years. Typically, fawns are born in early June, weighing approximately 3 kg at birth. Reproductive rates may be higher on Haida Gwaii, although reproductive data are limited. Sharpe (1999) suggested that on Haida Gwaii, onset of reproduction occurs in the first year, with females reproducing every year throughout their approximately 7- to 10-year life span. On Haida Gwaii, most litters tend to be of twins (range 1–3; Sharpe 1999).

Although weather can have both direct and indirect effects (e.g., on forage availability) on deer species in general (Connolly 1981), weather is likely far less important for black-tailed deer in coastal environments. This reduced effect may be greatest where natural predators are largely absent (e.g., Haida Gwaii), because snow, when present, will not influence predation success. Connolly (1981) argued that limitation of deer numbers in general results from a combination of weather, food supplies, predation (including hunting), parasites, disease, and human activities in deer habitats. Sharpe (1999) suggested that food and climate are the major factors controlling deer numbers in Haida Gwaii, but their combined effects are greatly reduced because of the absence of typical predators, such as wolves *Canis lupus* and mountain lions *Puma concolor*.

4.1 Importance of predation and competition

When predators are present, they can have significant impacts on populations of deer. Ninety percent of fecal samples from Alexander Archipelago wolves *Canis lupus ligoni* on Prince of Wales and adjacent islands, southeast Alaska, contained remains of Sitka black-tailed deer (n = 182; Kohira and Rexstad 1997). Deer remains occurred exclusively in 45% of the scats (Person et al. 1996). Coronation Island (southeast Alaska) has afforded the opportunity to monitor the dynamics of a Sitka black-tailed deer population first without, then with, and then again without wolves as predators (see Lewis 1992; Klein 1995): in 1960, wolves were introduced to Coronation, and the population of wolves grew quickly, along with the expected reduction in deer numbers and recovery of the vegetation; by the mid-1970s, wolves appeared to have died out on the island, and the deer population rebounded strongly by the late 1980s (see Kirchhoff and Person this volume).

In a recent review, Ballard et al. (2001) concluded that although predation by coyotes *Canis latrans*, mountain lions, and/or wolves may be a significant mortality factor for mule and black-tailed deer in some areas and under

some circumstances, there are very few published studies of the effects of predation on black-tailed deer, and most of them focused on Columbian black-tailed deer on Vancouver Island. Wolves are thought to have migrated in significant numbers to Vancouver Island in the 1970s to reestablish a viable population (Jones and Mason 1983; Atkinson and Janz 1994) and have been seen as a primary cause of the decline of the local Columbian black-tailed deer populations. Wolf control on Vancouver Island resulted in demographic changes (particularly increased recruitment to the adult populations) in the black-tailed deer population (Hatter 1988; Hatter and Janz 1994).

Black bears *Ursus americanus* and grizzly bears *Ursus arctos* are also known to take Sitka black-tailed deer, but the impacts of this predation are unstudied; this may be of particular interest on Haida Gwaii, where black bears are present, their impacts as predators on deer recognized but largely undocumented. The impact of predation is influenced by severe winters and changes in wintering habits as a result of forestry (B.C. Ministry of Environment, Lands, and Parks 2001). To help identify the relative effects of predation and other factors on black-tailed deer demography, 95 adult Columbian black-tailed deer were collared from February 1982 through June 1991 (McNay and Voller 1995). Deaths were from wolves, mountain lions, legal hunting and poaching, malnutrition, and accidents; wolves and mountain lions accounted for 61% of all deaths. Mountain lions were the most important predators. Predators concentrated on adult female deer from February through July. Very few adult deer died during summer, when both predators were presumably targeting fawns (McNay and Voller 1995). McNay and Voller (1995) argued that annual survival rates of resident deer at low elevations (73%) were not high enough to sustain populations. Of the 24 female fawns ($n = 12$) and yearlings ($n = 12$) with radio collars, only 1 fawn and 9 yearlings lived to become adults (McNay and Voller 1995). The overall survival rate of adult black-tailed deer was 74%, but migratory black-tailed deer had much higher survival (90%), presumably because resident deer remained at low elevations and were most prone to predation. Beyond the direct impact of predation, McNay and Voller (1995) emphasized that an essential condition to rebuild dwindling populations of Columbian black-tailed deer on Vancouver Island will be the amount of older intact forests left at low elevations. They concluded that forest harvesting (and associated activities) and spatial isolation of winter habitats may intensify predation on resident deer and impede recruitment of migrating deer. Besides affecting survival, predation (including hunting) also influences the behaviour of herbivores (Brown et al. 1999) and the way in which they can use or not use their habitat. On Haida Gwaii, regeneration of western redcedar *Thuja plicata* was much greater and overall deer impact lower in areas where deer were more exposed to hunting (Martin and Baltzinger 2002).

Competition is another possible extrinsic factor affecting black-tailed deer population dynamics. Sitka black-tailed deer, however, likely do not have significant competition from other ungulates. In areas of southeast Alaska where elk *Cervus elaphus* have been introduced (they also have been introduced on Haida Gwaii, where their diet has not been studied; see Golumbia et al. this volume), diets of deer and elk were similar during mild, relatively snow-free winters, with both species utilizing salal *Gaultheria shallon*, red huckleberry *Vaccinium parvifolium*, and western redcedar (Kirchhoff and Larsen 1998). Elk, however, ate more grasses (Poaceae) and sedges (Cyperaceae) than deer; deer ate more forbs and low-growing evergreen plants than elk (Kirchhoff and Larsen 1998).

4.2 Importance of cover and habitat

Throughout the range of Sitka black-tailed deer, cover is important for survival: to reduce energy expenditures for thermoregulation and for locomotion during periods of high snow cover, to limit food burial by snow, and to allow for escape and hiding from human and nonhuman predators (Nyberg et al. 1989). The coastal areas of northern British Columbia and southeast Alaska are made up of rugged mountains, high-rainfall forests, and thousands of kilometres of shoreline. Although there are occasional examples of large-scale blow-down in coastal forests, wind more commonly affects individual or small groups of trees, resulting in the maintenance of multiaged, diverse stands (Brady and Hanley 1984). Consequently, unlogged coastal old-growth forests are often characterized by a high frequency of low-impact disturbances that result in an interspersion of dense forest canopy with openings containing large amounts of available biomass for deer. This juxtaposition of habitats and forest edge is important to deer (Kirchhoff and Schoen 1983; Kremsater and Bunnell 1992), and their use of different seral stages and habitat types within coastal environments varies seasonally.

Throughout most of their range, the habitat of Sitka black-tailed deer has been affected by extraction of timber. Clearcuts produce large amounts of biomass in summer but offer little snow interception in winter, while the dense canopy of old-growth forests provides snow interception, as well as a litter of lichen and twigs. Several studies have demonstrated that snow can be a major factor influencing winter survival of Columbian black-tailed deer and Sitka black-tailed deer (Klein and Olson 1960; Bunnell et al. 1978; Jones and Mason 1983), both through the reduction of available forage (Harestad et al. 1982; Hanley and McKendrick 1983; Hovey and Harestad 1992) and because of the increased energetic costs of movement (Parker et al. 1984). Black-tailed deer sinking depth (Bunnell et al. 1990a,b) was greatest in clearcuts and intermediate in 20-year-old stands. It was lowest in old-growth and 80-year-old stands. The energy cost of moving through 25 cm of snow is about 2.5 times that of moving through 10 cm and increases as snowpacks become deeper (Parker et al. 1984). In southeast Alaska, when snow depth in the open was >15 cm, black-tailed deer concentrated their activities in the highest-volume old-growth stands available within their home ranges (Schoen and Kirchhoff 1990). In fact, during these severe winters, older forests were very important for the survival of deer (see Harestad 1980, 1985; Schoen et al. 1985), and persistent snow caused significant deer mortality. A severe winter with heavy, persistent snow in 1999 caused a large increase in the number of starvation-related mortalities of deer compared with the mild winter of 1997–1998 (Farmer and Person 1999).

Deer living in coastal forests, however, are usually exposed to only moderate snow depths, unlike those that can occur for interior populations of mule deer (e.g., Armleder et al. 1994). In addition, winter temperatures that frequently move above and below freezing can result in a discontinuous snow cover for much of the winter. Coastal environments also provide deer with relatively nonstressful thermal conditions in all seasons. The temperatures below which deer are thermally stressed and must begin to increase metabolic rates to maintain an acceptable body temperature vary with seasonal pelage (Parker 1988). In winter, the lower critical temperature for black-tailed deer is –6°C; in summer, it is +12°C. In some winter months in southeast Alaska, almost 40% of the weather observations showed that animals were thermally stressed (February; Parker et al. 1999), but animals were also frequently below their lower critical temperature in summer pelage in June (Parker et al. 1999). For much of the year, however, the percentage of time when animals were thermally stressed is quite low (Parker et al. 1999). Mean temperatures for Haida Gwaii are 11.4°C and 4.8°C for summer and winter, respectively (Environment Canada, based on St. James and Sandspit weather data), so deer on Haida Gwaii are also likely to be more affected by temperature when they are in summer pelage.

Old-growth and commercially exploited forests also differ greatly in their production of forage, in the protein digestibility of sun- and shade-grown leaves, and, consequently, in their relative abilities to support black-tailed deer populations (Hanley et al. 1989). On Vancouver Island, deer generally used young (6–45 years old) rather than old forests and tended to use young forests a high proportion of time (65–75% of locations) (McNay 1995). As long as suitable winter habitat is interspersed with different forest types, black-tailed deer populations survive well and, in many cases, reach higher densities than in undisturbed landscapes. In southeast Alaska, Sitka black-tailed deer select old-growth forest over even-aged, second-growth stands, particularly during winter (Wallmo and Schoen 1980; Rose 1982; Schoen and Kirchhoff 1985; Yeo and Peek 1992). These selection patterns have been explained by variation in forage abundance and availability (Wallmo and Schoen 1980), nutritional quality (Hanley et al. 1989), and snow accumulation (Kirchhoff and Schoen 1987).

During most seasons, it is likely that interspersion of habitats best explains the distribution of black-tailed deer. Research on the importance of edge to deer has produced equivocal results, but likely cannot be evaluated without consideration of local landscapes (Kirchhoff and Schoen 1983); the effects of edge appear less important when forage and cover are interspersed (Kremsater and Bunnell 1992). Sharpe (1999) suggested that large clearcuts benefit deer on Haida Gwaii only if they have a southerly aspect and therefore experience early snowmelt. Logging has likely contributed to increased deer numbers in some areas of Haida Gwaii, because openings have increased the amount of palatable forage available to black-tailed deer, while old-growth forest is often available to provide cover. The scale of forest conversion, particularly over the past 40 years, however, results in large areas of dense second growth that is not particularly good habitat for deer.

5. Patterns of movement

Although there are likely groups of both migratory and resident animals, as well as dispersal movements within populations of black-tailed deer (e.g., Bunnell and Harestad 1983; Harestad and Bunnell 1983), seasonal movements appear to be less important for Sitka black-tailed deer than for mule deer. Across a range of studies (e.g., Harestad 1980; Loft et al. 1984; Schoen and Kirchhoff 1985; McNay 1995; Boroski et al. 1999), home ranges varied from 12 to 500 ha, with migratory deer having larger home ranges than residents, in part because of their migratory behaviour. Deer living at low elevations on Vancouver Island tended to have smaller home ranges than animals at higher elevations (Harestad 1980). Nonmigratory populations of black-tailed deer in environments lacking heavy snow may be limited by forage conditions in late summer (Taber and Dasmann 1958); although vegetation is always available, the quality of the available food may be limiting.

On Admiralty Island, southeast Alaska, 75% of collared Sitka black-tailed deer ($n = 51$) made seasonal migrations from low-elevation winter ranges to high-elevation (usually subalpine or alpine) summer ranges; the remaining 25% were year-round residents at low elevations (Schoen and Kirchhoff 1985). In addition to making extensive movements between summer and winter ranges, migratory deer were located at higher elevations than resident deer during all seasons (Schoen and Kirchhoff 1985).

McNay (1995) and others collared 17 juvenile Columbian black-tailed deer to study dispersal patterns on Vancouver Island. Only 2 of the 17 deer dispersed to new ranges, and McNay (1995) suggested that young black-tailed deer rely on their mothers' expectations of future resources for their home range. McNay (1995) documented three "types" of dispersers: "regular" migrators, which spend long periods away from their natal ranges each year; "resident" deer, which always stay close to their natal ranges; and "irregular" migrators, which move away from their natal ranges less regularly and for shorter periods. Regular migrators had natal ranges at relatively high elevations, from which they travelled an average of 5.5 km to their alternative ranges. On Vancouver Island, severe winter conditions do not occur very often at the lowest elevations, and the deer monitored there remained at their natal ranges all year. This is similar to the situation with Haida Gwaii deer (see Gaston et al. this volume).

Water is also an important component of coastal environments. Deer frequently cross water bodies to move among archipelago islands. Black-tailed deer frequently traversed large reservoirs in California, typically in groups of 2–3 animals (Boroski et al. 1999); as many as 389 black-tailed deer swam across a reservoir during daylight in a single migration. In another Californian study, black-tailed deer frequently made crossings of reservoirs up to 1.6 km (Loft et al. 1984).

6. Nutrition, food habits, and energy requirements

Extensive field assessments of black-tailed deer food habits and nutrition are rare and difficult to obtain. Parker and coworkers (1999) conducted an intensive multiyear study of Sitka black-tailed deer on Channel Island (southeast Alaska); throughout this section, I rely heavily on those results. During their study, Sitka black-tailed deer were observed eating more than 70 different plant species, 39 of which were forbs (see Parker et al. 1999 for a comprehensive list and details of seasonal use). In that study, deer ate varying amounts of all plants reported in the study area, although some were eaten only opportunistically: Alaska yellow-cedar *Chamaecyparis nootkatensis*, which washed up on the beach of the island; and European mountain ash *Sorbus aucuparia* and highbush cranberry *Viburnum edule*, which grew only on one extremely steep and relatively inaccessible slope of the study site. Other species appeared to be "tested" for palatability and eaten rarely (e.g., Sitka spruce *Picea sitchensis*) (Parker et al. 1999).

In coastal forests, deer have access to the highest forage biomass in summer, in terms of both the amount of forbs and the availability of deciduous leaves. In winter, forage biomass is reduced, but low snow accumulation under dense forest overstory leaves evergreen forbs available throughout much of the winter. As a result, diets of deer are dominated by leaves and forbs in summer and shrubs, with the addition of evergreen forbs, in winter. In southeast Alaska, deer diets indicated a general preference for herbs (excluding graminoids) over shrubs and for shrubs over conifers throughout the year (Hanley and McKendrick 1985). When herb-layer forages were buried by snow and deer consumed a shrub-dominated diet, estimated dry matter digestibility of black-tailed deer diets decreased from 58% to 38%, and digestible energy explained diet selection (Hanley and McKendrick 1985). Analyses of species composition and quality of the diet of black-tailed deer and nutritional quality of forages indicated that digestible energy and digestible protein were probably the greatest nutritional limiting factors for deer in Alaska (Hanley and McKendrick 1985).

To a large extent, weather determines what food is available in winter to Sitka black-tailed deer (see Parker 1994): wind may make arboreal lichens (*Usnea* spp. and *Alectoria* spp.) available to deer; snow cover will determine the availability of evergreen forbs, such as bunchberry *Cornus canadensis*, five-leaved bramble *Rubus pedatus*, and foamflower *Tiarella trifoliata*, or woody stems of oval-leaved blueberry *Vaccinium ovalifolium* and Alaska blueberry *V. alaskaense*; and temperature alone (through freezing the ground) can determine the availability of fern (e.g., *Dryopteris dilatata*) rhizomes (Parker et al. 1999; Gillingham et al. 2000). Finally, retreating high tides frequently expose entire beach areas that are suddenly snow free and available to foraging animals (Parker et al. 1999).

Plant consumption also depends on temporal availability. When a range of mushroom species were available in the autumn, deer searched extensively for them; in winter, black-tailed deer searched for windblown lichens following major wind events during winter (Parker et al. 1999). In addition, the consumption of parts of some plant species depended on plant phenology. For example, deer consumed the fiddleheads of *Dryopteris* ferns in early spring, the green fern fronds during spring and summer, and the rhizomes in winter. Similarly, *Alnus* catkins and buds were eaten in early spring, the stems during winter, and the dried leaves in autumn. Other than *Carex* and *Fucus* spp., the numerous beach plants were all seasonally dependent forbs and therefore were not eaten during winter.

Overall, forbs, ferns, and skunk cabbage *Lysichiton americanum* constituted the largest component of dry matter intake by Sitka black-tailed deer in southeast Alaska during all months except January, February, and March (Parker et al. 1999). These forage species comprised 41–46% of the diet in September, November, December, and April; and 55–58% in August and October. From May through July, the herb-layer forages made up 69–74% of the diet eaten by Sitka black-tailed deer. Animals also ate large quantities of deciduous shrub leaves throughout the summer; in September, they consumed large amounts of fallen leaves (Malus and Alnus spp.). Between January and March, when herb-layer forages were covered in snow and contributed only 8% of the diet, deer ate primarily deciduous shrub stems and some conifer foliage. Shrub and conifer consumption was highest at 65% of the diet in January, declining to 42–47% in February and March (Parker et al. 1999).

Regardless of the foraging bout lengths and the lying bout times, black-tailed deer were active about 50% of the day throughout the year (Gillingham et al. 1997). In winter, the energy requirements exceeded intake for both male and female black-tailed deer (Parker et al. 1999)—regardless of how long the deer spent foraging or how far they travelled, the costs always exceeded the gains. In summer, however, food availability is higher and food quality is greater. Consequently, during summer, males were able to exceed requirements. For female black-tailed deer nursing twins, however, energy balance was also negative in midsummer at peak lactation (Parker et al. 1999). Females met their requirements (at that time, their intake rates were 50% higher than those of the males) only during spring and fall; this indicates the key contribution of body reserves to annual survival. Body reserves accumulated during summer with abundant digestible energy were critical to winter survival. In addition, body reserves are essential for survival in winter, because energy demands cannot be met by foraging alone; therefore, body reserves are used to make up the difference in surviving animals (Parker et al. 1999). In contrast, daily protein intake remained above demand during all months of the year except February, whereas deer were unable to meet energy requirements for more than half the year (Parker et al. 1999).

Body masses are generally highest in September through October and lowest in March. Body mass for mainland Sitka black-tailed deer shows a marked seasonal pattern, with declines in body mass ranging from 14% to 31% between October and March (Parker et al. 1993); the amount of mass lost over winter depends on the peak body mass attained during fall (Parker et al. 1993). Male black-tailed deer tend to have the highest percent body fat in October to November, just prior to peak rut in November, whereas female body condition is highest in late summer (Parker et al. 1999).

7. Impacts on vegetation

Exclosure studies have repeatedly shown that black-tailed deer have diverse impacts on their food plants, especially for longer-lived plant species (e.g., Stockton et al. 2001; Warner and Cushman 2002). This is particularly true when black-tailed deer are at high densities. In southeast Alaska, Klein (1965) observed that heavy use by Sitka black-tailed deer on Coronation Island resulted in a greatly reduced biomass of the forest understory; forage species preferred by black-tailed deer were nearly eliminated. Major impacts of deer on the forests of Haida Gwaii have been extensively described (Pojar and Banner 1984; Pojar 1999) and are the subject of many of the papers in this volume. Many of the highly utilized species from the mainland (see Parker et al. 1999), including Alaska blueberry, false azalea *Menziesia ferruginea*, spiny wood fern *Dryopteris dilatata*, bunchberry, five-leaved bramble, salmonberry *Rubus spectabilis*, devil's-club *Oplopanax horridus*, false lily-of-the-valley *Maianthemum dilatatum*, and skunk cabbage, are greatly reduced in their relative abundance on Haida Gwaii compared with the coastal mainland (Pojar 1999). Browsing by Sitka black-tailed deer introduced to Haida Gwaii has radically altered the vegetation of Haida Gwaii (B.C. Ministry of Forests 1980; this volume) and virtually eliminated most of the preferred forage species of black-tailed deer (Pojar 1999). Chemical and dendroecological analyses have recently been combined to demonstrate the relationship between deer density and the release of young Sitka spruce (Vila et al. 2002). Black-tailed deer may exert moderate to strong influences on the species composition and biomass of the forest understories, but their effect on dry matter digestibility, fibre, nitrogen, and phosphorus concentrations of individual species may be negligible (Hanley 1987).

Plants have evolved a number of methods of deterring herbivory, including physical defences, such as spines (e.g., devil's-club), and complex secondary compounds, such as terpenes (Connolly et al. 1980) and tannins (Robbins et al. 1987a,b; McArthur et al. 1993). Many of the forages that Sitka black-tailed deer consume have evolved such defences, although some of these defences may be reduced on Haida Gwaii (see Vourc'h et al. 2002). The amount and type of defensive compounds that plants develop in an attempt to deter herbivory depend on the conditions in which the plants are growing. For example, leaves of Alaska blueberry and bunchberry growing in three open clearcuts contained lower concentrations of nitrogen and higher concentrations of nonstructural carbohydrates and soluble phenolics (and greater astringency) than in two forests, but did not differ in *in vitro* dry matter digestibility (Hanley et al. 1987; Van Horne et al. 1988).

Black-tailed deer, however, have coevolved with these defences. Proteins in the saliva of deer bind to plant tannins to minimize absorption of tannins in the digestive tract and thus counteract the effects on digestibility (Robbins et al. 1987b; McArthur et al. 1993). In spring and summer, skunk cabbage can make up almost all of the diet of deer within some foraging bouts (Parker et al. 1999; Gillingham et al. 2001), despite the relatively high concentrations of cyanide. Black-tailed deer appear completely unaffected by these compounds and readily select skunk cabbage because of the high intake rate that they can achieve when eating large leaves. Another example of the adaptability of black-tailed deer is their extensive use of devil's-club despite the spines that cover the stems, petioles, and underside of the leaves. Deer consume these leaves from the top and are seemingly undeterred by this physical defence.

8. Conclusions

Across their range in British Columbia and Alaska, Sitka black-tailed deer populations are affected by weather, predation, habitat alterations, and energy limitation. The effects of these factors are interdependent. The effects of predation, for example, appear to be confounded by habitat alterations.

Black-tailed deer have a tremendous potential for rapid increases in number due to their early age of first reproduction, annual breeding, and capacity for twinning. This can be seen both in population recoveries after severe winters and in areas where they have recovered after predators have died out (e.g., Coronation Island). They are able to survive and reproduce in a system in which they can be in an energy deficit for much of the year. Their high reproductive rates combined with the absence of significant predation have resulted in the dramatic increase in Sitka black-tailed deer populations on Haida Gwaii over the last century and resultant effects on the native vegetation of Haida Gwaii described elsewhere in this volume. The likely presence of resident, migratory, and dispersing individuals within populations needs to be considered in terms of their ability to recolonize areas.

Black-tailed deer appear to be able to deal with a range of plant defences, and they can have a marked effect not only on the amount of plant biomass, but also on plant community structure. They can exploit a variety of habitats and consume a wide range of seasonally available forage species. Their life history is well timed to take advantage of the spring flush of foods that are high in energy and protein. Black-tailed deer appear to make the most of a relatively short period of time when they can consume more energy than they expend. This is demonstrated in their marked fluctuations in body mass and their ability to put on reserves to get through winter when forage availability is reduced, even in severely browsed systems. The challenges posed by Sitka black-tailed deer are in part due to the flexibility of black-tailed deer as a species.

Acknowledgements

Any review of information depends on those who have collected the original data and done the original studies—my thanks go to all those who have advanced our understanding of the ecology of black-tailed deer. The helpful comments of K.L. Parker, J.-L. Martin, T. Golumbia, and A.J. Gaston on drafts of this manuscript were greatly appreciated. Thanks also to the Research Group on Introduced Species for its financial support in getting me to the conference.

Literature cited

Armleder, H.M.; Waterhouse, M.J.; Keisker, D.G. 1994. Winter habitat use by mule deer in the central interior of British Columbia. Can. J. Zool. 72: 1721–1725.

Atkinson, K.T.; Janz, D.W. 1994. Effect of wolf control on black-tailed deer in the Nimpkish Valley on Vancouver Island. Wildlife Bulletin No. B-73, B.C. Ministry of Environment, Lands, and Parks, Nanaimo, B.C.

Ballard, W.B.; Lutz, D.; Keegan, T.W.; Carpenter, L.H.; deVos, J.C. 2001. Deer–predator relationships: a review of recent North American studies with emphasis on mule and black-tailed deer. Wildl. Soc. Bull. 29: 99–115.

B.C. Ministry of Environment, Lands, and Parks. 2001. Environmental Indicator 2000: Wildlife populations in British Columbia; final technical background document (February). Victoria, B.C. 29 pp.

B.C. Ministry of Forests. 1980. Relationships between introduced black-tailed deer and the plant life of the Queen Charlotte Islands, British Columbia. Smithers, B.C. 63 pp.

Boroski, B.B.; Barrett, R.H.; Kie, J.G. 1999. Movement patterns and survivorship of black-tailed deer migrating across Trinity Reservoir, California. Calif. Fish Game 85: 63–69.

Brady, W.W.; Hanley, T.A. 1984. The role of disturbance in old-growth forests: some theoretical implications for southeastern Alaska. Pages 213–218 *in* W.R. Meehan, T.R. Merrell, Jr., and T.A. Hanley (eds.), Fish and wildlife relationships in old-growth forests: Proceedings of a symposium held in Juneau, Alaska, 12–15 April 1982. American Institute of Fishery Research Biologists, Morehead City, North Carolina.

Brown, J.S.; Laundré, J.W.; Gurung, M. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. J. Mammal. 80: 385–399.

Bunnell, F.L.; Harestad, A.S. 1983. Dispersal and dispersion of black-tailed deer: models and observations. J. Mammal. 64: 201–209.

Bunnell, F.L.; Ellis, R.M.; Stevenson, S.K.; Eastman, D.S. 1978. Evaluating ungulate populations and range in British Columbia. Trans. N. Am. Wildl. Nat. Resour. Conf. 47: 311–322.

Bunnell, F.L.; Hovey, F.W.; McNay, R.S.; Parker, K.L. 1990a. Forest cover, snow conditions, and black-tailed deer sinking depths. Can. J. Zool. 68: 2403–2408.

Bunnell, F.L.; Parker, K.L.; McNay, R.S.; Hovey, F.W. 1990b. Sinking depths of black-tailed deer in snow, and their indices. Can. J. Zool. 68: 917–922.

Connolly, G.E. 1981. Limiting factors and population regulation. Pages 245–285 *in* O.C. Wallmo (ed.), Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln, Nebraska.

Connolly, G.E.; Ellison, B.O.; Fleming, J.W.; Geng, S.; Kepner, R.E.; Longhurst, W.M.; Oh, J.H.; Russell, G.F. 1980. Deer browsing of Douglas-fir trees in relation to volatile terpene composition and *in vitro* fermentability. For. Sci. 26: 179–193.

Farmer, C.J.; Person, D.K. 1999. Research progress report: Effect of even-aged timber management on survivorship of Sitka black-tailed deer. Federal Aid in Wildlife Restoration Project W-27-2, Job 14.16, Alaska Department of Fish and Game, Juneau, Alaska. 10 pp.

Gillingham, M.P.; Parker, K.L.; Hanley, T.A. 1997. Forage intake by black-tailed deer in a natural environment: bout dynamics. Can. J. Zool. 75: 1118–1128.

Gillingham, M.P.; Parker, K.L.; Hanley, T.A. 2000. Partial consumption of shield fern, *Dryopteris dilatata*, rhizomes by black-tailed deer, *Odocoileus hemionus sitkensis*, and its potential implications. Can. Field-Nat. 114: 21–25.

Gillingham, M.P.; Parker, K.L.; Hanley, T.A. 2001. Habitat use by black-tailed deer in relation to rate of forage intake. Alces 37: 339–352.

Hanley, T.A. 1984. Relationships between Sitka black-tailed deer and their habitat. General Technical Report PNW-168, Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture, Portland, Oregon. 27 pp.

Hanley, T.A. 1987. Physical and chemical response of understory vegetation to deer use in southeastern Alaska. Can. J. For. Res. 17: 195–199.

Hanley, T.A. 1993. Balancing economic development, biological conservation, and human culture: the Sitka black-tailed deer *Odocoileus hemionus sitkensis* as an ecological indicator. Biol. Conserv. 66: 61–67.

Hanley, T.A.; McKendrick, J.D. 1983. Seasonal changes in chemical composition and nutritive value of native forages in a spruce–hemlock forest, southeastern Alaska. Research Paper PNW-312, Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture, Portland, Oregon. 41 pp.

Hanley, T.A.; McKendrick, J.D. 1985. Potential nutritional limitations for black-tailed deer in a spruce–hemlock forest, southeastern Alaska. J. Wildl. Manage. 49: 103–114.

Hanley, T.A.; Cates, R.G.; Van Horne, B.; McKendrick, J.D. 1987. Forest stand-age-related differences in apparent nutritional quality of forage for deer in southeastern Alaska. Pages 9–17 *in* F.D. Provenza, J.T. Flinders, and E.D. McArthur (eds.), Plant–herbivore interactions: Proceedings of the 4th wildland shrub symposium, Snowbird, Utah, 7–9 August 1984. General Technical Report INT-222, Intermountain Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, Ogden, Utah.

Hanley, T.A.; Robbins, C.T.; Spalinger, D.E. 1989. Forest habitats and the nutritional ecology of Sitka black-tailed deer: a research synthesis with implications for forest management. General Technical Report PNW-230, Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture Portland, Oregon. 52 pp.

Harestad, A.S. 1980. Seasonal movements of black-tailed deer on North Vancouver Island. Fish and Wildlife Report No. R-3, B.C. Ministry of Environment, Victoria, B.C. 98 pp.

Harestad, A.S. 1985. Habitat use by black-tailed deer on northern Vancouver Island. J. Wildl. Manage. 49: 946–950.

Harestad, A.S.; Bunnell, F.L. 1983. Dispersal of a yearling male black-tailed deer. Northwest Sci. 57: 45–48.

Harestad, A.S.; Rochelle, J.A.; Bunnell, F.L. 1982. Old-growth forests and black-tailed deer on Vancouver Island. Trans. N. Am. Wildl. Nat. Resour. Conf. 47: 343–353.

Hatter, I.W. 1988. Effects of wolf predation on recruitment of black-tailed deer on northeastern Vancouver Island. Fish and Wildlife Report No. R-23, B.C. Ministry of Environment, Victoria, B.C. 82 pp.

Hatter, I.W.; Janz, D.W. 1994. Apparent demographic changes in black-tailed deer associated with wolf control on northern Vancouver Island. Can. J. Zool. 72: 878–884.

Hovey, F.W.; Harestad, A.S. 1992. Estimating effects of snow on shrub availability for black-tailed deer in southwestern British Columbia. Wildl. Soc. Bull. 20: 308–313.

Jones, G.W.; Mason, B. 1983. Relationship among wolves, hunting, and population trends of black-tailed deer in the Nimpkish Valley on Vancouver Island. Fish and Wildlife Report No. R-7, B.C. Ministry of Environment, Victoria, B.C. 26 pp.

Kie, J.G.; Bowyer, R.T.; Nicholson, M.C. 2002. Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. Ecology 83: 530–544.

Kirchhoff, M.D.; Larsen, D.N. 1998. Dietary overlap between native Sitka black-tailed deer and introduced elk in southeast Alaska. J. Wildl. Manage. 62: 236–242.

Kirchhoff, M.D.; Schoen, J.W. 1983. Black-tailed deer use in relation to forest clear-cut edges in southeastern Alaska. J. Wildl. Manage. 47: 497–501.

Kirchhoff, M.D.; Schoen, J.W. 1987. Forest cover and snow: Implications for deer habitat in southeast Alaska. J. Wildl. Manage. 51: 28–33.

Klein, D.R. 1965. Ecology of deer range in Alaska. Ecol. Monogr. 35: 259–284.

Klein, D.R. 1995. The introduction, increase, and demise of wolves on Coronation Island, Alaska. Pages 275–280 *in* L.N. Carbyn, S.H. Fritts, and D.R. Seip (eds.), Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University of Alberta, Edmonton, Alberta.

Klein, D.R.; Olson, S.T. 1960. Natural mortality patterns of deer in southeast Alaska. J. Wildl. Manage. 24: 80–88.

Kohira, M.; Rexstad, E.A. 1997. Diets of wolves, *Canis lupus*, in logged and unlogged forests of southeastern Alaska. Can. Field-Nat. 111: 429–435.

Krausmann, P.R. 1994. The subspecies. Page 251 *in* D. Gerlach, S. Atwater, and J. Schnell (eds.), The wildlife series: Deer. Stackpole Books, Mechanicsburg, Pennsylvania.

Kremsater, L.L.; Bunnell, F.L. 1992. Testing responses to forest edges: the example of black-tailed deer. Can. J. Zool. 70: 2426–2435.

Lewis, S.W. 1992. Relationships between deer and vegetation on Coronation Island, southeastern Alaska. M.Sc. thesis, University of Alaska, Fairbanks, Alaska. 93 pp.

Loft, E.R.; Menke, J.W.; Burton, T.S. 1984. Seasonal movements and summer habitats of female black-tailed deer. J. Wildl. Manage. 48: 1317–1325.

Martin, J.-L.; Baltzinger, C. 2002. Interaction among deer browsing, hunting, and tree regeneration. Can. J. For. Res. 32: 1254–1264.

Martin, J.-L.; Daufresne, T. 1999. Introduced species and their impacts on the forest ecosystem of Haida Gwaii. Pages 69–85 *in* G.G. Wiggins (ed.), Proceedings of the cedar symposium: growing western redcedar and yellow-cypress on the Queen Charlotte Islands/Haida Gwaii. B.C. Ministry of Forests/ Canada–British Columbia South Moresby Forest Replacement Account, Victoria, B.C.

McArthur, C.; Robbins, C.T.; Hagerman, A.E.; Hanley, T.A. 1993. Diet selection by a ruminant generalist browser in relation to plant chemistry. Can. J. Zool. 71: 2236–2243.

McCullough, D.R. 1997. Breeding by female fawns in black-tailed deer. Wildl. Soc. Bull. 25: 296–297.

McNay, R.S. 1995. The ecology of movements made by Columbian black-tailed deer. Ph.D. thesis, University of British Columbia, Vancouver, B.C. 194 pp.

McNay, R.S.; Voller, J.M. 1995. Mortality causes and survival estimates for adult female Columbian black-tailed deer. J. Wildl. Manage. 59: 138–146.

McTaggart-Cowan, I. 1945. The ecological relationships of the food of the Columbian black-tailed deer in the coast forest region of southern Vancouver Island, B.C. Ecol. Monogr. 15: 110–139.

McTaggart-Cowan, I. 1956. Life and times of the coast black-tailed deer. Pages 523–617 *in* W.P. Taylor (ed.), The deer of North America. Stackpole Books, Harrisburg, Pennsylvania.

Nelson, R. 1997. Heart and blood: Living with deer in America. Alfred A. Knopf, New York. 389 pp.

Nyberg, J.B.; McNay, R.S.; Kirchhoff, M.K.; Forbes, R.; Bunnell, F.; Richardson, E. 1989. Integrated management of timber and deer: coastal forests of British Columbia and Alaska. General Technical Report PNW GTR 226, Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture, Portland, Oregon. 65 pp.

Parker, K.L. 1988. Effects of heat, cold, and rain on coastal black-tailed deer. Can. J. Zool. 66: 2475–2483.

Parker, K.L. 1994. The cost of living. Pages 306–314 *in* D. Gerlach, S. Atwater, and J. Schnell (eds.), The wildlife series: Deer. Stackpole Books, Mechanicsburg, Pennsylvania.

Parker, K.L.; Robbins, C.T.; Hanley, T.A. 1984. Energy expenditures for locomotion by mule deer and elk. J. Wildl. Manage. 48: 474–488.

Parker, K.L.; Gillingham, M.P.; Hanley, T.A.; Robbins, C.T. 1993. Seasonal patterns in body mass, body composition, and water transfer rates of free-ranging and captive black-tailed deer (*Odocoileus hemionus sitkensis*) in Alaska. Can. J. Zool. 71: 1397–1404.

Parker, K.L.; Gillingham, M.P.; Hanley, T.A.; Robbins, C.T. 1996. Foraging efficiency: energy expenditure versus energy gain in free-ranging black-tailed deer. Can. J. Zool. 74: 442–450.

Parker, K.L.; Gillingham, M.P.; Hanley, T.A.; Robbins, C.T. 1999. Energy and protein balance of free-ranging black-tailed deer in a natural forest environment. Wildl. Monogr. 143: 5–48.

Person, D.K.; Kirchhoff, M.D.; Van Ballenberghe, V.; Iverson, G.C.; Grossman, E. 1996. The Alexander Archipelago wolf: a conservation assessment. General Technical Report PNW-384, Pacific Northwest Research Station, Forest Service, U.S. Department of Agriculture, Portland, Oregon. 42 pp.

Pojar, J. 1999. The effects of deer browsing on the plant life of Haida Gwaii. Pages 90–98 *in* G.G. Wiggins (ed.), Proceedings of the cedar symposium: growing western redcedar and yellow-cypress on the Queen Charlotte Islands/Haida Gwaii. B.C. Ministry of Forests/Canada–British Columbia South Moresby Forest Replacement Account, Victoria, B.C.

Pojar, J.; Banner, A. 1984. Old-growth forests and introduced black-tailed deer on the Queen Charlotte Islands, British Columbia. Pages 247–257 *in* W.R. Meehan, T.R. Merrell, Jr., and T.A. Hanley (eds.), Fish and wildlife relationships in old-growth forests: Proceedings of a symposium held in Juneau, Alaska, 12–15 April 1982. American Institute of Fishery Research Biologists, Morehead City, North Carolina.

Robbins, C.T.; Hanley, T.A.; Hagerman, A.E.; Hjeljord, O.; Baker, D.L.; Schwartz, C.C.; Mautz, W.W. 1987a. Role of tannins in defending plants against ruminants: reduction in protein availability. Ecology 68: 98–107.

Robbins, C.T.; Mole, S.; Hagerman, A.E.; Hanley, T.A. 1987b. Role of tannins in defending plants against ruminants: reduction in dry matter digestion? Ecology 68: 1606–1615.

Rose, C.L. 1982. Deer response to forest succession on Annette Island, southeast Alaska. M.Sc. thesis, University of Alaska, Fairbanks, Alaska. 56 pp.

Schoen, J.W.; Kirchhoff, M.D. 1985. Seasonal distribution and home-range patterns of Sitka black-tailed deer on Admiralty Island, southeast Alaska. J. Wildl. Manage. 49: 96–103.

Schoen, J.W.; Kirchhoff, M.D. 1990. Seasonal habitat use by Sitka black-tailed deer on Admiralty Island, Alaska. J. Wildl. Manage. 54: 371–378.

Schoen, J.W.; Wallmo, O.C.; Kirchhoff, M.D. 1981. Wildlife–forest relationships: Is a reevaluation of old growth necessary. Trans. N. Am. Wildl. Nat. Resour. Conf. 46: 531–544.

Schoen, J.W.; Kirchhoff, M.D.; Thomas, M.H. 1985. Seasonal distribution and habitat use by Sitka black-tailed deer in southeastern Alaska. Federal Aid in Wildlife Research Final Report, Project W-17-11, W-21-1, W-21-2, W-22-3, and W-22-4, Alaska Department of Fish and Game, Juneau, Alaska. 44 pp.

Shackleton, D.M. 1999. Hoofed mammals of British Columbia. Royal British Columbia Museum Handbook 3, University of British Columbia Press, Vancouver, B.C. 268 pp.

Sharpe, S. 1999. Management of deer on the Queen Charlotte Islands: Biology of the species. Pages 118–124 *in* G.G. Wiggins (ed.), Proceedings of the Cedar Symposium: growing western redcedar and yellow-cypress on the Queen Charlotte Islands/Haida Gwaii. B.C. Ministry of Forests/Canada–British Columbia South Moresby Forest Replacement Account, Victoria, B.C.

Stockton, S.; Gaston, A.J.; Martin, J.-L. 2001. Where are all the flowers gone? The impact of introduced black tailed deer on the shoreline vegetation of Haida Gwaii, British Columbia. Pages 31–42 *in* A.J. Gaston (ed.), Laskeek Bay Research 10. Laskeek Bay Conservation Society, Queen Charlotte City, B.C.

Taber, R.D.; Dasmann, R.F. 1958. The black-tailed deer of the chaparral/its life history and management in the north coast range of California. Game Bulletin No. 8, California Department of Fish and Game, Sacramento, California. 163 pp.

Van Horne, B.; Hanley, T.A.; Cates, R.G.; McKendrick, J.D.; Horner, J.D. 1988. Influence of seral stage and season on leaf chemistry of southeastern Alaska deer forage. Can. J. For. Res. 18: 90–99.

Vila, B.; Vourc'h, G.; Gillon, D.; Martin, J.-L.; Guibal, F. 2002. Is escaping deer browse just a matter of time in *Picea sitchensis*? A chemical and dendroecological approach. Trees – Struct. Funct. 16: 488–496.

Vourc'h, G.; Vila, B.; Gillon, D.; Escarré, J.; Guibal, F.; Fritz, H.; Clausen, T.P.; Martin, J.-L. 2002. Disentangling the causes of damage variation by deer browsing on young *Thuja plicata*. A chemical and dendrochronological approach. Oikos 98: 271–283.

Wallmo, O.C. (ed.). 1981a. Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln, Nebraska.

Wallmo, O.C. 1981b. Mule and black-tailed deer distribution and habitats. Pages 1–25 *in* O.C. Wallmo (ed.), Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln, Nebraska.

Wallmo, O.C.; Schoen, J.W. (eds.). 1979. Sitka black-tailed deer: proceedings of a conference held in Juneau, Alaska. Forest Service, U.S. Department of Agriculture, Alaska Region.

Wallmo, O.C.; Schoen, J.W. 1980. Response of deer to secondary forest succession in southeast Alaska. For. Sci. 26: 448–462.

Warner, P.J.; Cushman, J.H. 2002. Influence of herbivores on a perennial plant: variation with life history stage and herbivore species. Oecologia 132: 77–85.

Yeo, J.J.; Peek, J.M. 1992. Habitat selection by female Sitka black-tailed deer in logged forests of southeastern Alaska. J. Wildl. Manage. 56: 253–261.

A conceptual framework for introduced species research in Haida Gwaii

Anthony J. Gaston and Jean-Louis Martin

Abstract

The introduction of alien species to islands by people has been ongoing for millennia. In the case of Haida Gwaii (Queen Charlotte Islands, British Columbia), most introductions were deliberate. All alien arrivals have consequences for indigenous biota. Our attitudes towards such introductions depend on a cost–benefit analysis in which very different currencies (biological, economic, cultural, aesthetic) need to be combined. We discuss the role of research in providing evidence for such decision-making and stress the value of biodiversity as a general measure of biological health.

> Rational conservation policy must recognize the forces of change and the grander scale of things, including situations where no management is possible or necessary. Biological conservation is not synonymous with preservation, or maintaining the status quo, but with sensible wildlife management in a dynamic environment constantly being altered by man.
>
> —King (1984:190)

1. Introduction

People have been moving animals and plants around the planet with them for a long time. The dingo, the Australian wild dog, is believed to have been carried to Australia about 1500 BC (Diamond 1997). Canoes, populating the far-flung islands of the Pacific, brought chickens, pigs, and Polynesian rats *Rattus exulans* to Melanesia by 1500 BC and to Hawaii by 500 AD (Jennings 1979; Atkinson 1985).

People transfer organisms outside their normal ranges either accidentally, like rats coming ashore from shipwrecks, or deliberately, as was the case with deer, squirrels, and raccoons in Haida Gwaii (Queen Charlotte Islands, British Columbia). Introductions may be as domestic animals or as deliberate attempts at naturalization. Some domestic introductions subsequently go wild, as was the case for rabbits in Britain and for cattle in Haida Gwaii. However, most introduced species that have become established in Haida Gwaii arrived as a result of deliberate attempts at naturalization. Of the important mammalian introductions to this archipelago, only the rats arrived accidentally.

Among those imported to Haida Gwaii, not all have prospered. Neither of the two large deer introduced—Rocky Mountain elk *Cervus elaphus nelsoni* and European red deer *Cervus elaphus elaphus*—has prospered, although elk persist in small numbers. Thankfully, cats, dogs, and rabbits remain largely domestic here: that has not always been the case elsewhere (Moors and Atkinson 1984; Moors 1985). Likewise, of the many plant species introduced since the arrival of Europeans, most are confined, so far, to areas heavily disturbed by human activities: roadsides, clearcuts, pastures, and gardens. Only a small minority of the organisms that have been brought into the Islands have become widely naturalized—that is, self-sustaining—within naturally occurring ecosystems. It is this group and their impacts on the ecosystems within which they survive that have formed the basis for the work of the Research Group on Introduced Species (RGIS).

2. The value of introduced species research—fundamental

The topic of plant and animal introductions has been of great interest to biologists, because introductions provide accidental ecological experiments (Elton 1958; Vitousek 1990). As deliberate novel perturbations of ecosystems, introductions can yield important information on the way in which ecosystems cope with rapid change. In some cases, they provide useful tests for predictions based on theories of ecosystem functioning (Vitousek 1990). In others, they may reveal unexpected connections within ecosystems that lead us to develop new ideas or test old ones about the interrelations between different ecosystem components or between species (Moulton and Pimm 1983; Vitousek 1990; Simberloff et al. 2000). We hope that our work in Haida Gwaii, especially that of the graduate students, whose theses are necessarily dedicated to the advancement of fundamental knowledge, has contributed to a better understanding of terrestrial ecosystems in general. This should become clear from succeeding papers.

3. The value of introduced species research—practical

It is a truism in ecology that everything has some effect. The energy entering an ecosystem is fixed by solar

radiation and by fluxes from neighbouring ecosystems; space is also finite. Any new arrival can exist only at the expense of some preexisting element. So, "did such and such an introduction affect existing ecosystems?" is not a useful question. We need to ask instead:

1. How has the introduction affected native ecosystems?
2. What is the magnitude of the changes created?
3. What is the trajectory of change, and what is the likely endpoint?
4. What has been the value gained?
5. What has been the value lost?

Given money and time, science can provide fairly unequivocal answers to the first two questions. Science can also give some provisional answers to the third question, although ecologists know that predictions are perilous, given the fluctuating environmental context. All these questions will be dealt with in the succeeding papers in this volume.

Questions 4 and 5 are about what we value in an ecosystem or a landscape. They can be answered only by the community at large through the expression of their joint will, either deliberately, as in creating regulations and policies, or accidentally, by ignoring the problem and allowing simple economics to determine the outcome. This has been dealt with extensively by Simberloff (this volume).

In the course of our research, the RGIS has attempted to quantify changes in the vegetation of Haida Gwaii as a result of the introduction of the Sitka black-tailed deer *Odocoileus hemionus sitkensis*. Our emphasis has been partly on the western redcedar *Thuja plicata*, because of its economic and cultural significance. This is a subject that has already received a lot of attention (Wiggins 1999). However, a larger effort has been applied to assessing the effect of the deer on the overall biodiversity of native forest ecosystems.

Biodiversity is a concept that synthesizes the different kinds of diversity that occur among ecosystems, whether temperate rainforests or those that develop in an unwashed coffee mug. Among biologists, changes in biodiversity within a given ecosystem are used as indicators of ecosystem health. A decrease in the biodiversity of a given area is regarded as lowering its biological value, because it is believed to lower productivity and ecosystem stability, hence making the ecosystem more vulnerable to further degradation (Simberloff and Van Holle 1999; Cabin et al. 2000). By making the effects on biodiversity central to the RGIS research strategy, we have sought to develop as broad a picture as possible of changes that have affected local ecosystems.

In most studied cases, the biological impact of introductions has been found to be negative (loss of diversity), whereas the economic and cultural value may be positive. This is an equation in which decisions need to be made on the basis of criteria that rank in very different value systems. How we, as biologists, value ecosystems and how we regard declines in biodiversity are obviously going to be affected by our interest in the living world. However, by investigating the biodiversity changes that have occurred in the wake of expanding deer populations in Haida Gwaii, we hope to provide evidence on which informed choices can be made about future courses of action. As individuals, we may have particular attitudes or agendas with respect to the deer in Haida Gwaii, but in our research, we attempt to provide the best possible information on the biological costs and benefits of introductions. We can certainly contribute to the formation of strategies for action or inaction, but our main role is to provide the evidence.

There is one school of thought that feels further research on deer in Haida Gwaii is unnecessary. Deer have an obvious impact on forest regeneration, and this makes them a pest, their pest status being heightened by the fact that they were introduced to the islands and hence "foreign." If the forests were arable cropland, we would accept the need for culling deer as a price of growing food, and individual farmers would invest more or less in deer exclusion or control, according to their own analysis of the economic costs incurred. However, forests, even commercially exploited forests, are seen increasingly as having amenity values above their purely economic value. We may expect a shift in decisions relating to deer control from the economic pest model towards more multiuse appraisals of costs and benefits, including the benefits drawn from deer harvested from these areas. Information obtained by RGIS on deer behaviour, on the impact of browsing on early tree growth, and on the possible value of chemical defences, in the case of the redcedar, probably can make a useful contribution to economic calculations relating to the impact of deer on managed forests. Other information on biodiversity impact and cascade effects within forest ecosystems is relevant to a broader approach to the problem.

Many of RGIS's findings have been on the impacts that deer have had on forest ecosystems not affected by forestry or other intensive resource extraction. Hence, our contribution is of direct relevance in deciding what, if any, management strategy for deer should be adopted on the remaining wildlands of Haida Gwaii. However, as will become increasingly clear throughout this volume, the ecosystem simplification resulting from overabundant deer populations can be seen as symptomatic of the consequences of any simplification of forest ecosystems (e.g., by intensive forestry or by the removal of top predators) on the biological complexity of forest ecosystems. In the rest of this paper, we deal with the conceptual framework within which such forest management strategies can be developed.

4. Some case studies

4.1 The rabbit

Rabbits *Oryctolagus cuniculus* were introduced into England in the 12th century as semidomesticated animals (Sheail 1971). Once they became naturalized, they developed into important ecosystem architects. Their grazing maintains a very low, dense sward and promotes the survival of dwarf or low-growing plant species, while preventing the encroachment of shrubs. Rabbit-grazed heath supports a characteristic vegetation and forms a distinctive landscape feature. In addition, rabbits form important nodes in the food web. Where abundant, they are the principal prey of Common Buzzards *Buteo buteo* and stoats *Mustela erminea*.

They are also important diet items for harriers (*Circus* spp.), red foxes *Vulpes vulpes*, and European badgers *Meles meles*. The myxomatosis virus was introduced in 1953 and wiped out 99% of the rabbit population within a year. The roads in some areas were slick with squashed rabbits (the disease first blinded them). Since then, the rabbit has gradually developed resistance to the disease and is now almost back to its former status, hardier than ever.

There are several points that we can note from this history lesson: the rabbit adapted to local conditions only after a substantial time had elapsed (several centuries); it became important prey for some native predators and created a distinctive scenery that supports a characteristic flora; the introduction of an exceptionally virulent and species-specific disease gave a respite of only a few decades, while causing enormous suffering and conditions that would not be considered acceptable in the current animal rights climate (AJG, exposed to the event as a child, found it to be traumatic).

4.2 The ship, roof, or black rat and the brown rat

The genus *Rattus* originated in Asia, and two species became cosmopolitan human commensals: the variously named black, roof, or ship rat *R. rattus* and the larger brown or Norway rat *R. norvegicus*. The black rat is the major intermediate host in human outbreaks of the bubonic plague virus. It occurs in several morphs, including the dark grey "black" rat and the paler "Alexandrine" rat.

For the most part, rats remain associated with human activities, living on stored food, garbage, or agricultural wastes (Corbet 1966). However, black rats became naturalized on many isolated islands from tropical to subpolar regions, living on vegetation, birds, and, in some cases, intertidal life (Atkinson 1985). Latterly, over much of its former range, the black rat has been supplanted by the larger and more aggressive brown rat, and, during the second half of the 18th and the early 19th century, black rats disappeared from most of Europe, except for seaports. A similar competitive exclusion occurred wherever brown rats followed black rats in establishing themselves in temperate and cold climates, although the two species coexist on many temperate or tropical oceanic islands (Atkinson 1985). On the islands where they occur, black rats have often profoundly affected nesting bird populations, reducing their abundance (Penloup et al. 1997), affecting community assemblages (Martin et al. 2000), and driving entire groups of species or subspecies to extinction (Thibault et al. 2002).

Regarding rats on remote islands, we can note here that they did not create any diversification of landscape, nor did they form the basis for any important food chains, except for other imported species; they had a strong effect in reducing the diversity of birds and, in some cases, insects and plants; and their role as disease vectors and association with garbage mean they get little sympathy—this undoubtedly increases the acceptability of eradication among the public.

4.3 Raccoons in Haida Gwaii

Raccoons *Procyon lotor* were introduced into the Islands in the 1940s to create an additional source of furs for trappers (Carl and Guiget 1972). They expanded throughout the archipelago and have reached almost all islands not separated by at least 600 m of water from potential stepping stones (Hartman 1993; Golumbia et al. this volume). Currently, their pelts have little commercial value, and few are trapped locally (personal communications from local residents). They do not form an important prey base for any predator.

On small islands that support seabird colonies, raccoons may become specialists in killing adult seabirds (Rodway 1991; Gaston and Masselink 1997; Hartman et al. 1997), particularly burrow-nesting auks (Rhinoceros Auklet *Cerorhinca monocerata*, Cassin's Auklet *Ptychoramphus aleuticus*, Ancient Murrelet *Synthliboramphus antiquus*), which they have extirpated from several islands (Rodway et al. 1988; Gaston and Masselink 1997). Raccoons also reduce the reproductive success of coastal-nesting birds, such as Glaucous-winged Gulls *Larus glaucescens* and Black Oystercatchers *Haematopus bachmani* (Vermeer et al. 1997), and probably also Semipalmated Plovers *Charadrius semipalmatus* (Cooper and Miller 1997). Their impact on intertidal life is unknown, but requires investigation.

The impact of raccoons on seabirds led to an interagency agreement to eradicate them from one important colony island (by shooting), to monitor further invasions, and to conduct further eradications, if necessary. Potential jump-off sites on the main islands were also monitored and culled periodically. To date, this policy seems to have prevented further erosion of seabird colonies.

We note that action was taken in response to threatened bird populations of international significance; eradications were local; and to date, the consequences of this introduction for the intertidal and other ecosystems of Haida Gwaii are unknown.

4.4 Contrasts

The comparison of these three introductions with the situation following the introduction of black-tailed deer in Haida Gwaii is instructive. The impact of rabbits on nonagricultural land promoted certain types of landscape at the expense of others and provided conditions for certain plants and animals to flourish. Time and money were expended to try to maintain the preexisting situation. When rabbits were decimated by myxomatosis, people generally found the resulting ecosystem changes, with heathland reverting to scrub, to be undesirable. At the scale of the whole countryside, rabbits added diversity, both biological and scenic. They were also good to eat, although they went out of fashion when they became too common. It is unlikely that any further attempts at eradication will be made in Britain, although control on agricultural land is ongoing.

The case of rats has been different. Throughout large parts of their range, they remained largely commensals of human activities. They had no beneficial effects, either on flora or on landscape. Their impact on biodiversity was mostly negative. When they invaded small islands, they

became predatory and strongly affected local bird diversity. In Haida Gwaii, they have been considered harmful to the native biota, and much effort has been expended to eradicate them. This effort continues, and total eradication from Haida Gwaii appears a feasible and desirable prospect.

Concerning raccoons, information to date suggests that their main impact is on seabirds that breed only on certain small islands. Local control by shooting—a more humane method than poisoning and one that avoids nontarget species—appears to be adequate to cope with the situation. Further research to determine consequences for other biological communities would be highly desirable and might change our attitude towards the raccoons.

5. Costs and benefits of deer in Haida Gwaii

Turning to deer, we find that their effects in Haida Gwaii have some beneficial and some harmful elements. They have undoubtedly brought about a significant change in landscapes. The open understory that Pojar refers to in the first paper of this volume is a striking feature of the old-growth forests more or less throughout Haida Gwaii, as is the dense regeneration of western hemlock *Tsuga heterophylla* and, in places, Sitka spruce *Picea sitchensis* (Vila and Martin this volume). In clearings along the coast, especially on sunny south faces, deer seem to be responsible for maintaining grassy meadows that form such an attractive feature of places such as Vertical Point on Louise Island. The bonsai Sitka spruce associated with such clearings form a distinctive landscape feature. All these changes probably add to the attractiveness of the archipelago to tourists: impenetrable shrubs reduce the accessibility and visibility of the forest interior and the availability of camping sites. There is evidence that people prefer a mixed landscape of clearings and forest over undiluted forest cover as an idealized habitat (Wilson 1984; Kellert and Wilson 1993). The ease with which fresh venison can be obtained is undoubtedly a social and economic benefit.

On the debit side, deer have a strong impact on forest regeneration, promoting hemlock and spruce at the expense of redcedar (Martin and Baltzinger 2002), but slowing their growth (Vila et al. 2001, 2002, 2003). They also have a very obvious effect on the diversity of shrubs and wildflowers (Stockton this volume) and on the associated insects (Allombert and Martin this volume) and birds (Martin, Allombert, and Gaston this volume). Some of the plants and birds affected are races unique to Haida Gwaii. Some of the insects affected have been found in the archipelago only where deer are absent. The most heavily impacted areas, of which Reef, Kunga, and Ramsay islands provide good examples, are exceptionally low in biodiversity, except where steep cliffs or gullies prevent deer from reaching the vegetation. Wildflowers are virtually absent, drastically reducing the numbers of large insects and hummingbirds. Except for the large trees and litter decomposers, they are virtual biological deserts. Whether the current sparseness of some original ecosystem elements, such as the Haida ermine *Mustela erminea haidarum* and the local race of the Northern Goshawk *Accipiter gentiles laingi*, can be attributed to changes brought about by deer, we do not know. However, forest songbirds are likely to have been important diet items for both species, and these have certainly been reduced following the arrival of deer (Martin, Allombert, and Gaston this volume). The reduction or loss of important medicinal, food, and fibre plants used for cultural activities by the Haida people has been considerable (sections 3.1 and 3.5 in Golumbia and Rowsell this volume).

Then there is the loss of former landscapes. Today, the appearance and structure of the landscape a century ago can be gleaned only from a handful of archived diaries and manuscripts, a few photographs, and the memories of a few elders. Photographs and accounts of Haida Gwaii before the arrival of deer describe shoreline areas clothed in very dense stands of salmonberry *Rubus spectabilis*, thimbleberry *Rubus parviflorus*, red elder *Sambucus racemosa*, and other shrubs. Interior forests were known to be dense with thickets of salal *Gaultheria shallon* and devil's-club *Oplopanax horridus*. RGIS experiments suggest that both the shoreline and forest interior communities are highly modified. These changes signal a loss of history.

Where clearcutting or the conversion of land for farming has taken place in the islands, we cannot expect most native plants and animals to thrive. New ecosystems have been created to which many native organisms are less well adapted than immigrants from areas where disturbance and agriculture have been ongoing for longer. Trying to prevent the spread of nonnative plants and animals in these areas may have little value in protecting history or culture—and even, probably, little biological value. The main concern in the case of these species is their potential for proliferation and eventual invasion of natural ecosystems. Such invasions occur unpredictably, sometimes long after the original introduction, and mean that we have to be concerned about all exotics (Simberloff this volume).

On the other hand, the ecosystems native to Haida Gwaii represent unique associations of plants and animals. Our research suggests that their uniqueness stems, in part, from an initial absence of large mammalian herbivores, creating conditions under which certain plants and animals became dominant. This arrangement is an accident of history: if deer had been present in the area of the Hecate Strait land bridge in the late Pleistocene, they would no doubt have been native to the Islands. If deer had been present at that time, then presumably their predators would also have been there, providing the same balance found on the mainland. As a result, the vegetation there would be very similar to that of mainland coastal forests.

During the final day of this meeting, we considered options for deer management in the Islands. In doing so, several elements were recognized in the debate. Firstly, like rabbits in the United Kingdom, deer are neither an undiluted boon nor an unalloyed pest. This makes for an interesting debate—indeed, it is probably the only reason why we are having a debate at all. Secondly, the treatment of managed forests and natural forests may vary, because the values, and hence the arguments for and against control, differ. Thirdly, biological arguments in favour of deer control derive mainly from their impact on biodiversity—a fairly recent concept, the importance of which is still subject to debate (Tilman 1999, 2000; Chapin et al. 2000; McCann 2000). Biodiversity changes may be very cryptic, either because the objects

of study are fairly obscure (insects, snails) or because the impact of the deer is so widespread and all-pervasive that there is no real basis on which their impact can be measured. As a consequence, the case of the black-tailed deer in Haida Gwaii illustrates a situation where careful and intensive research is required to illustrate the true biological cost of the introduction, which can then be applied, with other considerations, to management decision-making.

Literature cited

Atkinson, I.A.E. 1985. The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas. Pages 35–81 *in* P.J. Moors (ed.), Conservation of island birds. Technical Publication No. 3, International Council for Bird Preservation, Cambridge, U.K.

Cabin, R.J.; Weller, S.G.; Lorence, D.H.; Flynn, T.W.; Sakai, A.K.; Sandquist, D.; Hadway, L.J. 2000. Effects of long-term ungulate exclusion and recent alien species control on the preservation and restoration of a Hawaiian tropical dry forest. Conserv. Biol. 14: 439–453.

Carl, G.C.; Guiget, C.J. 1972. Alien animals in British Columbia. B.C. Provincial Museum Handbook 14, Victoria, B.C. 94 pp.

Chapin, F.S., III; Zavaleta, E.S.; Eviner, V.T.; Naylor, R.L.; Vitousek, P.M.; Reynolds, H.L.; Hooper, D.U.; Lavorel, S.; Sala, O.E.; Hobbie, S.E.; Mack, M.C.; Díaz, S. 2000. Consequences of changing biodiversity. Nature (London) 405: 234–242.

Cooper, J.M.; Miller, E.H. 1997. Populations, status and biology of shorebirds breeding near Masset, Queen Charlotte Islands. Pages 123–129 *in* K. Vermeer and K.H. Morgan (eds.), The ecology, status, and conservation of marine and shoreline birds of the Queen Charlotte Islands. Occasional Paper No. 93, Canadian Wildlife Service, Ottawa, Ontario.

Corbet, G.B. 1966. The terrestrial mammals of Western Europe. Foulis & Co., London, U.K.

Diamond, J. 1997. Guns, germs and steel: the fates of human societies. Norton, New York.

Elton, C. 1958. The ecology of invasions by animals and plants. Methuen, London, U.K.

Gaston, A.J.; Masselink, M. 1997. The impact of raccoons, *Procyon lotor*, on breeding seabirds at Englefield Bay, Haida Gwaii, Canada. Bird Conserv. Int. 7: 35–51.

Hartman, L.H. 1993. Ecology of coastal raccoons (*Procyon lotor*) on the Queen Charlotte Islands, British Columbia, and evaluation of their potential impact on native burrow-nesting seabirds. M.Sc. thesis, University of Victoria, Victoria, B.C.

Hartman, L.; Gaston, A.J.; Eastman, D. 1997. Raccoon predation on Ancient Murrelets on East Limestone Island, British Columbia. J. Wildl. Manage. 61: 377–388.

Jennings, J.D. (ed.). 1979. The prehistory of Polynesia. Harvard University Press, Cambridge, Massachusetts.

Kellert, S.R.; Wilson, E.O. (eds.). 1993. The biophilia hypothesis. Island Press/Shearwater Books, Washington, D.C.

King, C. 1984. Immigrant killers: introduced predators and the conservation of birds in New Zealand. Oxford University Press, Aukland, New Zealand.

Martin, J.-L.; Baltzinger, C. 2002. Interaction among deer browsing, hunting, and tree regeneration. Can. J. For. Res. 32: 1254–1264.

Martin, J.L.; Thibault, J.C.; Bretagnolle, V. 2000. Black rats, island characteristics and colonial nesting birds in the Mediterranean: current consequences of an ancient introduction. Conserv. Biol. 14: 1452–1466.

McCann, K.S. 2000. The diversity–stability debate. Nature (London) 405: 228–233.

Moors, P.J. (ed.). 1985. Conservation of island birds. Technical Publication No. 3, International Council for Bird Preservation, Cambridge, U.K.

Moors, P.J.; Atkinson, I.A.E. 1984. Predation on seabirds by introduced animals and factors affecting its severity. Technical Publication No. 2, International Council for Bird Preservation, Cambridge, U.K.

Moulton, M.P.; Pimm, S.L. 1983. The introduced Hawaiian avifauna: biogeographic evidence for competition. Am. Nat. 121: 669–690.

Penloup, A.; Martin, J.L.; Gory, G.; Brunstein, D.; Bretagnolle, V. 1997. Nest site quality and nest predation as factors explaining the distribution of pallid swifts (*Apus pallidus*) on Mediterranean islands. Oikos 80: 78–88.

Rodway, M.S. 1991. Status and conservation of breeding seabirds in British Columbia. Pages 43–102 *in* J.P. Croxall (ed.), Seabird status and conservation: a supplement. International Council for Bird Preservation, Cambridge, U.K.

Rodway, M.S.; Lemon, M.J.F.; Kaiser, G.W. 1988. British Columbia seabird colony inventory. Report No. 1: East coast of Moresby Island. Technical Report Series No. 50, Canadian Wildlife Service, Pacific and Yukon Region, Delta, B.C. 275 pp.

Sheail, J. 1971. Rabbits and their history. David & Charles, London, U.K.

Simberloff, D.; Van Holle, B. 1999. Positive interactions of nonindigenous species: invasional meltdown? Biol. Invasions 1: 21–32.

Simberloff, D.; Dayan, T.; Jones, C.; Ogura, G. 2000. Character displacement and release in the small Indian mongoose, *Herpestes javanicus*. Ecology 81: 2086–2099.

Thibault, J.C.; Martin, J.-L.; Penloup, A.; Meyer, J.Y. 2002. The role of introduced animals in the extinction of Polynesian monarchs. Biol. Conserv. 108: 161–174.

Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. Ecology 80: 1455–1474.

Tilman, D. 2000. Causes, consequences and ethics of biodiversity. Nature (London) 405: 208–211.

Vermeer, K.; Morgan, K.H.; Smith, G.E.J. 1997. Oystercatcher habitat selection, reproductive success and their relationship with Glaucous-winged Gulls. Colon. Waterbirds 15: 14–23.

Vila, B.; Keller, T.; Guibal, F. 2001. Influence of browsing cessation on *Picea sitchensis* radial growth. Ann. For. Sci. 58: 853–859.

Vila, B.; Vourc'h, G.; Gillon, D.; Martin, J.-L.; Guibal, F. 2002. Is escaping deer browse just a matter of time in *Picea sitchensis*? A chemical and dendroecological approach. Trees–Struct. Funct. 16: 488–496.

Vila, B.; Guibal, F.; Torre, F.; Martin, J.-L. 2003. Growth change of young *Picea sitchensis* in response to deer browsing. For. Ecol. Manage. 201: 171–185.

Vitousek, P.M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Oikos 57: 7–13.

Wiggins, G.G. (ed.). 1999. Proceedings of the cedar symposium: growing western redcedar and yellow-cypress on the Queen Charlotte Islands/Haida Gwaii. B.C. Ministry of Forests/ Canada–British Columbia South Moresby Forest Replacement Account, Victoria, B.C.

Wilson, E.O. 1984. Biophilia. Harvard University Press, Cambridge, Massachusetts.

Lessons from the Islands

Top left:
Caption: Field camp, Reef Island
Credit: RGIS, Jean-Louis Martin

Top centre:
Caption: Cafeteria experiment
Credit: RGIS, Gwenaël Vourc'h

Top right:
Caption: Sorting insect samples
Credit: RGIS, Jean-Louis Martin

Middle left:
Caption: Measuring a Varied Thrush
Credit: RGIS, Jean-Louis Martin

Middle centre:
Caption: Vegetation inventory near exclosure
Credit: RGIS, Jean-Louis Martin

Middle right:
Caption: Tree section with rub scars caused by deer
Credit: RGIS, Bruno Vila

Bottom:
Caption: Bird's-eye view of Laskeek Bay
Credit: Gowgaia Institute, Box 638, Queen Charlotte, Haida Gwaii, Canada V0T 1S0, www.spruceroots.org

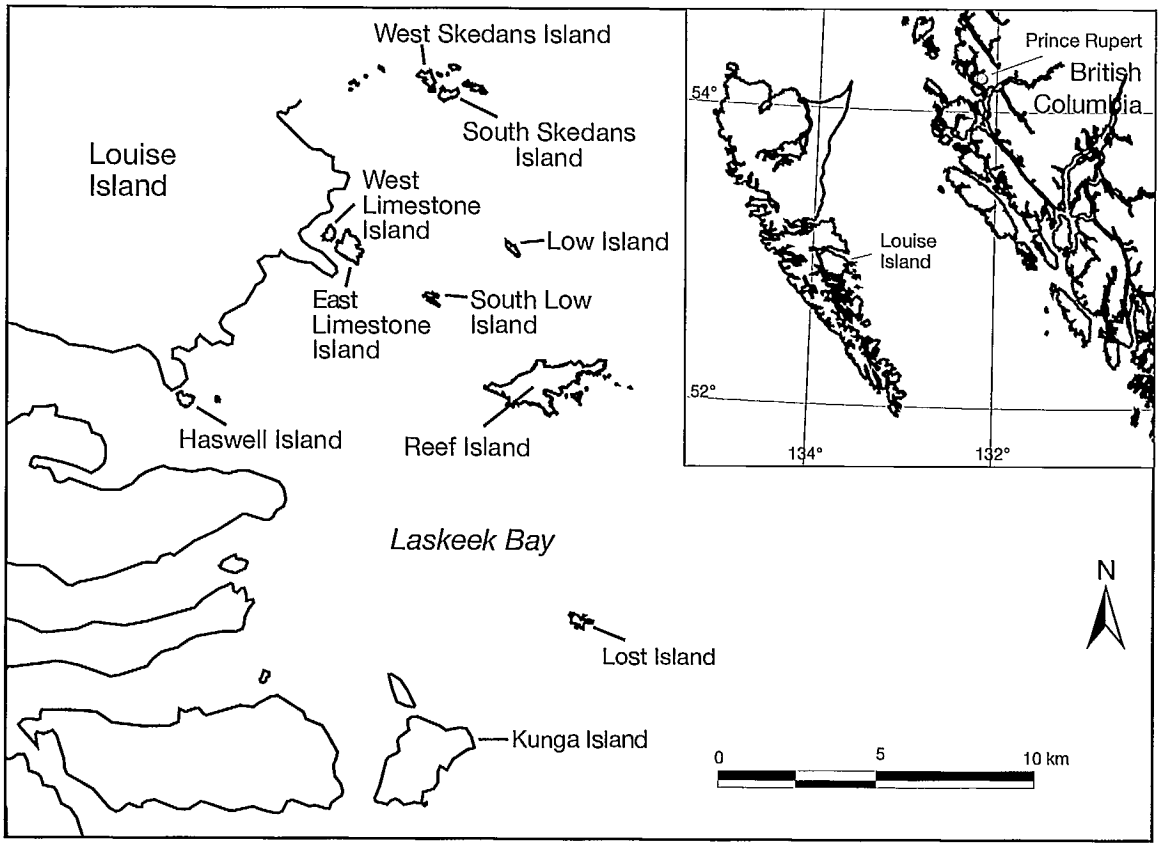
Introduction to the terrestrial ecology of Laskeek Bay

Stephen A. Stockton and Anthony J. Gaston

Laskeek Bay, on the east coast of Haida Gwaii (Queen Charlotte Islands, British Columbia), was the main study area for the Research Group on Introduced Species during 1996–2002. It contains 15 islands of varying size dispersed at varying distances from one another. Our main study sites comprised 10 islands (Fig. 1), of which Reef Island (249 ha), the farthest offshore of any island more than 100 ha in extent, was chosen for deer eradication (Gaston et al. this volume). Two other larger islands, Kunga Island (395 ha) and East Limestone Island (41 ha), were used as control sites for the deer removal experiment. The remaining seven islands—Haswell, West Limestone, West Skedans, South Skedans, Low, South Low, and Lost—were used for a comparative study of deer impacts. All these smaller islands are located within 17 km of one another and range in area from 4.5 ha to 16 ha (Table 1). West Limestone Island, West Skedans and South Skedans islands, and South Low and Low islands are part of a British Columbia Wildlife Management Area, whereas Lost Island falls within the perimeter of Gwaii Haanas National Park Reserve and Haida Heritage Site. Some additional research was carried out at the southeast corner of Louise Island, the largest island in Laskeek Bay (25 000 ha), and on Graham Island in the north.

All of the islands of Laskeek Bay support temperate coniferous forest, dominated by Sitka spruce *Picea sitchensis* on the smallest and most offshore islands and by western

Figure 1
Map of Haida Gwaii and Laskeek Bay, showing the "laboratory" islands, the deer cull islands, and the deer cull control sites



hemlock *Tsuga heterophylla* and spruce elsewhere. Varying amounts of western redcedar *Thuja plicata* occur on all islands except Lost and South Low. Small amounts of shore pine *Pinus contorta* var. *contorta* occur on southerly aspects on Reef Island. Small groves of Pacific crab apple *Malus fusca* scattered throughout Laskeek Bay are mainly associated with previous Haida occupation sites. None of the 10 islands studied has been commercially logged, and all maintain primary forest cover. Generally, the islands we studied were too small and rugged to support significant wetlands or streams. Consequently, we could collect little information on those ecosystems.

Small areas of nonforest habitat occur on exposed coasts, where they support either a diverse sward of forbs and low shrubs or a rather uniform tussock grass meadow of Nootka reed-grass *Calamagrostis nootkaensis*. The latter is best developed on the eastern end of Reef Island.

We obtained estimates of the duration of deer presence on the different islands in Laskeek Bay (Table 1) from comparative analyses of shrub stem age structures and the dating of fraying scars (Vila and Martin this volume). South Low, Low, and Lost islands showed no sign of deer, past or present. West Skedans and South Skedans islands showed evidence of deer for less than 20 years. Reef, Kunga, East Limestone and West Limestone, and Haswell islands all showed evidence of deer presence for more than 50 years.

In addition to deer, introduced red squirrels *Tamiasciurus hudsonicus* and raccoons *Procyon lotor* occur in Laskeek Bay. Both species occur on Louise, East Limestone, and West Limestone islands, although raccoons were eradicated from East Limestone Island in 1992 and have been only sporadic visitors since.

Table 1
Characteristics of the seven small islands in Laskeek Bay making up the natural laboratory, showing deer duration, determined by tree ring analysis showing first instance of deer "rub scars" (see Vila et al. 2002), island area, and island isolation (distance to Louise Island in main island chain) (both from Martin et al. 1995)

Island	Deer duration (years)	Island area (ha)	Island isolation: distance to Louise Island (m)
Haswell	>50	13.3	150
West Limestone	>50	16.0	350
West Skedans	<20	8.2	1350
South Skedans	<20	5.6	2400
South Low	None	4.5	2900
Low	None	9.6	5400
Lost	None	5.3	7300

Literature cited

Martin, J.-L.; Gaston, A.J.; Hitier, S. 1995. The effect of island size and isolation on old growth forest habitat and bird diversity in Gwaii Haanas (Queen Charlotte Islands, Canada). Oikos 72: 115–131.

Vila, B.; Vourc'h, G.; Martin, J.-L.; Guibal, F. 2002. Is escaping deer browse just a matter of time in *Picea sitchensis*? A chemical and dendroecological approach. Trees – Struct. Funct. 16: 488–496.

Spread and history of deer impact: the memory of the woody plants

Bruno Vila and Jean-Louis Martin

Abstract

Dendrochronology provides information on temporal and spatial variation of ecological events affecting a given site, information that is especially valuable in the absence of more traditional sources of information. Trees and shrubs can record, in the form of signatures in their woody structure, the impact of deer and other browsing animals. We use these signatures to understand the colonization of the Haida Gwaii (Queen Charlotte Islands, British Columbia) archipelago by deer and variation in the intensity of browsing pressure over time and space. The signatures occur in the form of fraying scars or shape modifications on trees and shrubs and cause important modifications of growth and stem age structures. These modifications vary according to the capacity of the species and of each individual plant, in terms of chemical or physical defences. They show that the presence of deer leads to changes in forest dynamics by favouring Sitka spruce *Picea sitchensis* at the expense of western hemlock *Tsuga heterophylla* and even more of western redcedar *Thuja plicata* and to the progressive and, eventually, total disappearance of shrubs from the understory. Changes in shrub stem age structures show that the deer started to have a strong impact on the archipelago approximately 40 years ago, although much local variation occurs. Fraying scars, a more accurate signature of deer colonization, suggest that impact on the understory became severe up to two decades after colonization occurred. The results suggest that the colonization of the archipelago was fast and that the pressure of the deer has increased continuously since colonization.

1. Introduction

Tree ring series are a natural data storage system containing valuable ecological and historical information that can be unlocked with the use of appropriate "keys." This information, which often cannot be obtained from other repositories, gives dendrochronology its unique role in providing data for the interpretation of past environments and historical events or for the interpretation of ecological parameters, such as past and present forest disturbances (Banks 1991).

Disturbances occur in all ecosystems; they may be chronic, intermittent, or infrequent, and they can be categorized as geomorphic, climatic, or biotic. Their frequency and intensity may be specific to tree, tree age, tree species, or stand, or they may be nonspecific, affecting forests over large geographic regions (Banks 1991). The disturbances of highest interest in dendrochronology are those that produce observable and measurable changes in one or more tree ring attributes (Schweingruber 1988, 1996).

Among the disturbances caused by biotic factors are the explosions of herbivore populations. They can be triggered by natural processes or result from imbalances caused by human activities, such as species introductions. Whatever their origin, these disturbances cause stress to trees and shrubs and leave traces in ring series. When the particular species involved in the disturbance is identified and its signature on the ligneous component understood, a correlation between the presence/abundance of that species and the intensity of the signature can be established (Schweingruber 1988, 1996).

Ungulates are among the major species able to leave signatures on plants. Dendrochronologists have been using signatures left in tree ring series to study spatial and temporal variation in the abundance of several animal species (Payette 1987; Bordage and Filion 1988; Morneau and Payette 1998, 2000). Motta (1995, 1996, 1997) studied the age and distributions of fraying or bark-stripping scars left by ungulates in alpine forests to develop a temporal understanding of ungulate population dynamics.

The Haida Gwaii archipelago (Queen Charlotte Islands, British Columbia) provides a unique opportunity to develop such a study because of the introduction of the Sitka black-tailed deer *Odocoileus hemionus sitkensis* Merriam in the late 19th century. Understanding the ecological role of this introduced species has become a major focus of research and a major concern for local communities and managers in recent years. It was felt essential to develop a better knowledge of the spread and intensity of browsing history from the regional scale to the scale of local plant populations and of individual plants within these populations. To address these questions, the signatures that deer have left in the wood are probably the most widespread and reliable source of information, assuming that we can develop the tools to read them. The work presented here will give an overview of the tools developed by this study and what they have taught us about how deer have affected and will affect woody plants on Haida Gwaii.

2. The signatures left by deer

The drastic changes in abundance and cover of the vegetation on Haida Gwaii have been emphasized repeatedly (Pojar et al. 1980; Pojar this volume, on vegetation changes in historical time; Stockton this volume). These changes result from repeated damage to foliage, twigs, and bark and from antler rubbing, leading to the development of a browsing limit in the understory at 1–1.5 m above the ground (Vila et al. 2001, 2003a,b; Vila 2002; Vourc'h et al. 2002).

2.1 On regenerating and adult trees

Below the browsing limit, the shape of regenerating trees is often very compact, as a result of intense branching. When the apex of such stunted trees surpasses the browsing limit, the tree resumes a normal development of trunks and branches that contrasts with the short branched and compacted lower part. Trunks below the browsing limit are sometimes sinusoidal and multistemmed (Fig. 1; Vila et al. 2001, 2003a,b).

Deer can also leave scars on young or adult trees (or on stems of large shrubs) as a result of bark stripping during winter, when forage is rare, or of fraying, when bucks rub their antlers against trees or shrubs during the rut or when shedding velvet. Scars are easy to recognize. They are produced on the stems by local debarking, which causes lesions and stops ring formation. The scars we observed in our study area were essentially from fraying. Among trees, western redcedar *Thuja plicata* was the preferred species. Willow (*Salix* sp.) and red alder *Alnus rubra* were used in the absence of western redcedar. Among trees, deer select those with a circumference of less than 50 cm. On each damaged tree, between two and three scars were usually recorded.

Figure 1
Schematic representation of stunted spruce that are heavily browsed and smaller than the browsing limit and escaped spruces that have exceeded the browsing limit. Escaped spruces display a stunted shape under the browsing limit and a normal shape above it. Trunks under the browsing limit are sometimes sinusoidal and multi-stemmed (from Vila et al. 2002).

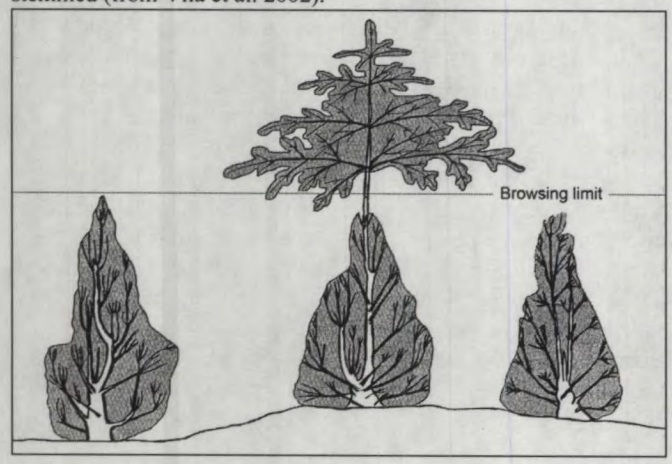


Figure 2
Fraying scar induced by deer on western redcedar

Scars occur on the trunk between 35 and 70 cm above the ground. They average 35 cm in length and 5–6 cm in width (Fig. 2; Vila et al. 2004a).

2.2 On shrubs

The shape of shrubs is markedly modified by repeated browsing. In red huckleberry *Vaccinium parvifolium*, for instance, in the absence of deer, the rate of sprouting is low but sufficient to compensate for the death of the older stems. When huckleberry is heavily browsed, regenerating shoots keep emerging from the lignotuber but are systematically browsed. The stumps of these browsed shoots accumulate at the base of the few surviving stems that were tall enough to have foliage beyond the reach of deer. As a result, the average number of stems per individual is significantly larger on deer-free islands (mean ± SE, 7.8 ± 1.4) than on deer-affected islands (2.0 ± 0.2), and the average number of shoots per individual is significantly smaller on deer-free islands (0.9 ± 0.5) than on deer-affected islands (9.3 ± 1.1) (Vila et al. 2004b).

3. How do deer affect forest dynamics?

3.1 Deer impact on trees

3.1.1 Regenerating and adult trees

Browsing and fraying cause shape modifications and exposure to disease. Height and radial growth are also particularly altered. For example, browsing of foliage induces a drastic decrease in radial growth in salal *Gaultheria shallon* shrubs (Vila et al. 2005). One of the most dramatic illustrations of the impact that deer have on plant growth and development is provided by the changes observed when regenerating trees succeed in reaching the browsing limit and manage to escape deer browsing (Fig. 3). The growth pattern of these trees is characterized by 1) an initial phase of stagnation in growth (phase 1) with narrow rings (<0.5 mm/year); 2) an abrupt increase in ring width once the tree has reached the browsing limit (phase 2); and 3) a growth stabilization characterized by wider rings (1–3 mm/year), which gradually replaces the phase of growth increase (phase 3). Vila et al. (2003a) showed clearly how this radial growth pattern and the correlated variation in tree shape are strictly controlled by deer browsing.

The narrow rings, which correspond to the period of intense browsing, can be used to 1) quantify the consequences of browsing on radial and height growth, 2) understand the mechanisms involved in escaping deer browsing, and 3) assess growth indices when deer are present and estimate the delay that deer cause in tree recruitment (Vila et al. 2001, 2003a,b; Vila 2002).

Mean radial growth of escaped trees was about seven times larger above the browsing limit than below the browsing limit (Fig. 4). Mean height growth of escaped trees was almost two times larger above the browsing limit than under the browsing limit (Fig. 4). These differences quantify the amount of growth lost to deer browsing and vary with the species considered (Vila 2002; Vila et al. 2002, 2003a,b; Vourc'h et al. 2002). They cause delays in tree regeneration. At our study sites, it took approximately 13 years for a spruce (on Reef and East Limestone islands) and 20 years for a hemlock (Koya Bay on Moresby Island) to reach the height of about 1.20 m that was necessary to isolate the apical bud from deer reach. On the basis of the work of Coates et al. (1985) on Haida Gwaii, showing that an unbrowsed tree needs only 5 years to reach a height of 1.10 m, we conclude that intense browsing by deer can delay sapling recruitment by at least 8 years for spruce (Vila et al. 2003a) and 15 years for hemlock (Vila et al. 2003b) under the deer densities and conditions where we sampled.

The mechanisms involved in tree response to browsing varied with tree species. In Sitka spruce, age was the main factor. Small, heavily browsed trees are simply younger than escaped trees and will ultimately reach the browsing limit (Vila 2002; Vila et al. 2002). As the tree gains height and width, the apical bud gets increasing protection from the sharp mature leaves that characterize this species, as well as from the rigidity of its stem.

For western redcedar, age was not the sole factor involved. The ability to grow and escape also seemed to depend on the capacity of a given tree to produce enough chemical defences to deter deer from browsing it (see Vila 2002; Vourc'h et al. 2002 and this volume; Vila et al. 2003a). In this species, the soft leaves and flexible stems offer little protection against deer.

In western hemlock, the delays we observed before escaping were longer than those observed for the escaped trees from the two other conifer species (Vila et al. 2003b). The soft needles and flexible stem make this species more

Figure 3
Radial growth pattern showing the typical variation in ring widths with time in four escaped Sitka spruces sampled on West Limestone Island (from Vila et al. 2003a)

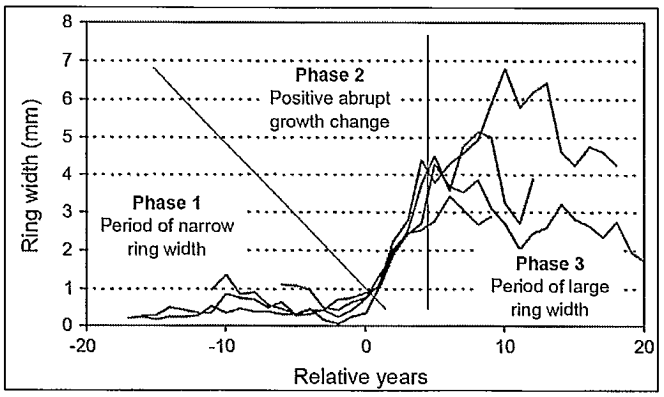
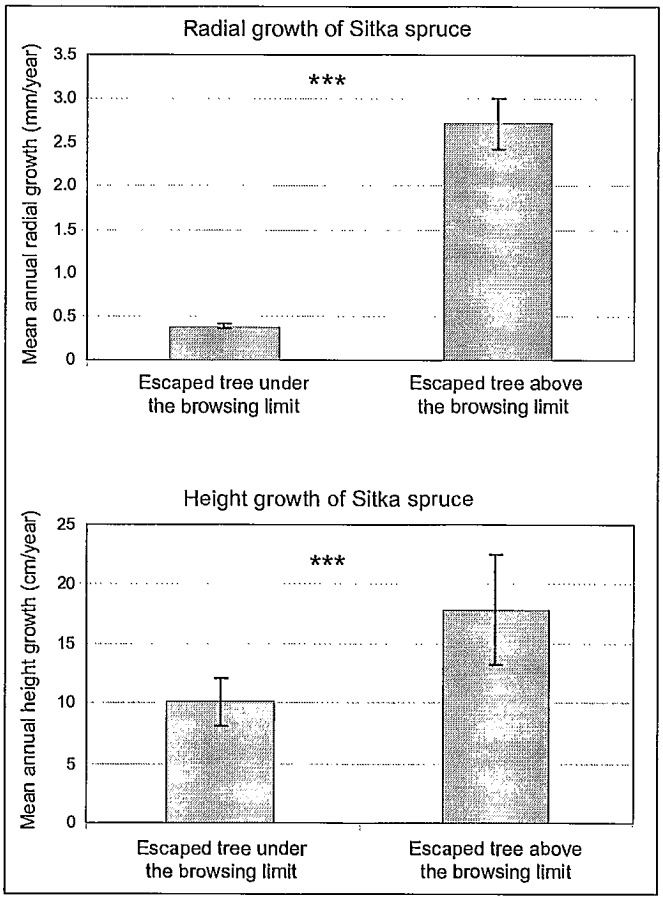


Figure 4
Radial and height growth indices of Sitka spruce under and above the browsing limit, showing the amount of growth lost to deer browsing. Vertical bars are standard error. *** = $P < 0.001$ (from Vila et al. 2003a).



vulnerable to deer than Sitka spruce (Vila et al. 2003a). On the other hand, when alternative forage is available, this species is less affected by browsing (Martin and Baltzinger 2002). We have no data on the chemistry of stunted and escaped trees that we found growing side by side.

Lesions such as those produced by fraying expose the plant to diseases. On Reef Island, 91.2% of western redcedars with fraying scars had insect galleries and/or decayed wood above the scar. Only 8.8% of western redcedars were not altered. When the wood decays, cavities appear in the trunk. No sign of compartmentalization (confinement of discoloured wood) was found on western redcedars (Fig. 5). On South Skedans Island, all trees studied presented discoloured wood above the scar, but no decayed wood or cavities were observed. All trees sampled showed signs of compartmentalization (Fig. 6). Large differences existed between species. The mean number of years necessary to close a scar with a mean size typical of each species was about 13 years for alder, 15 years for willow, and 29 years for western redcedar. This absence of compartmentalization associated with a slow process of healing favours wood decay. In the case of western redcedar, this lack of compartmentalization may lead to the loss of the tree affected from the future population of mature trees (Vila et al. 2004a).

3.1.2 Long-term effect of deer on forest dynamics

Our results confirm the hypothesis of Pojar and Banner (1984) suggesting that the severe impact of deer would probably cause the extinction of western redcedar as a commercial timber species on Haida Gwaii and increase damage to Sitka spruce and western hemlock. At current levels of deer pressure, our analysis also supports previous work (Coates et al. 1985; Martin and Daufresne 1999; Martin and Baltzinger 2002; Vila 2002; Vourc'h et al. 2002; Vila et al. 2003a,b; Research Group on Introduced Species, unpubl. data) suggesting that western redcedar regeneration has ceased in old-growth forests. Deer fraying has also had a retroactive effect on the growth of some of the young western redcedar trees that were already established before deer colonization (Vila et al. 2004a). Western redcedar regeneration is much restricted in secondary forests (Martin and Baltzinger 2002), where its future abundance may depend on the amount of deer hunting (Martin and Baltzinger 2002). As deer browsing causes longer delays in the growth of western hemlock than of Sitka spruce under heavy browsing pressure, this could even lead, locally, to an increased proportion of Sitka spruce relative to western hemlock (Vila 2002).

Figure 5
Cross-section of a western redcedar characterized by decaying wood and the absence of compartmentalization

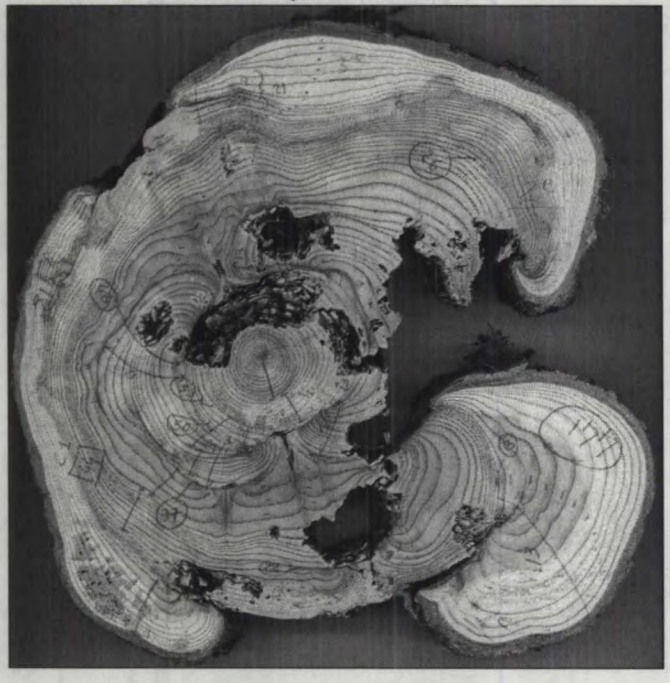
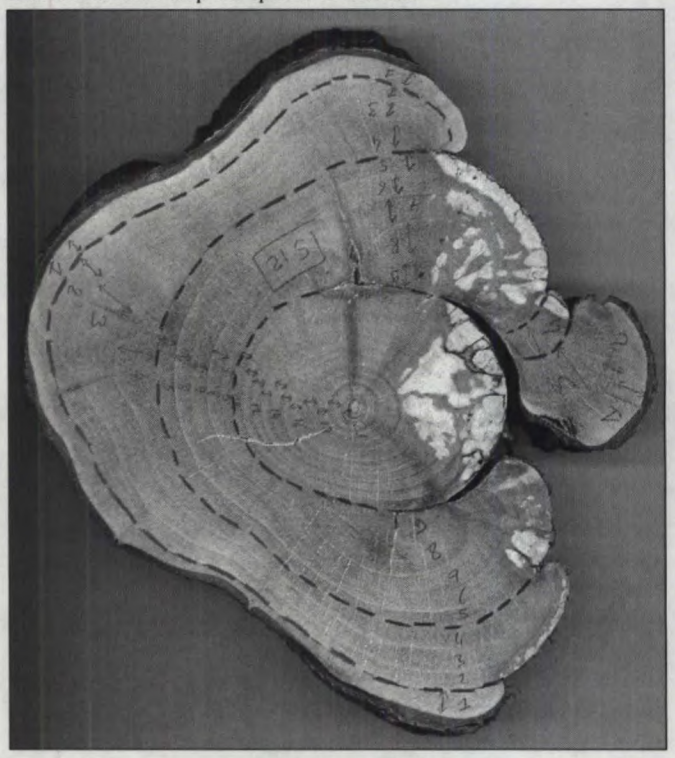


Figure 6
Consequences of deer fraying on wood integrity and tree health. Cross-section of a willow shows discoloration and compartmentalization to stop the spread of disease.



3.2 Shrub dynamics: an understory of the living dead?

We analyzed deer impact on shrubs by the study of stem age structures. The age structure of shrub stems is heavily modified by the absence of stem recruitment caused by shoot browsing. In the absence of deer, stems die at an average age of 25.2 ± 15.1 years and are regularly replaced by new shoots. When deer are present, this regular process of stem replacement is stopped, and the stems tall enough to escape deer will continue to grow and age. The average age of these old stems is 57.8 ± 16.3 years. Eventually, aging stems die off, nutrient reserves of the lignotuber get exhausted, and the plant dies (Vila et al. 2004b). Similarly, browsing prevents young plants born from seeds from

growing. These observations suggest that in the studied understories of mature forests with deer, the shrub population is currently a population of elderly plants slowly fading away as individuals die, one after the other, of old age (Vila et al. 2004b).

4. Can we reconstruct the history of deer colonization?

4.1 Can we date deer impact and colonization?

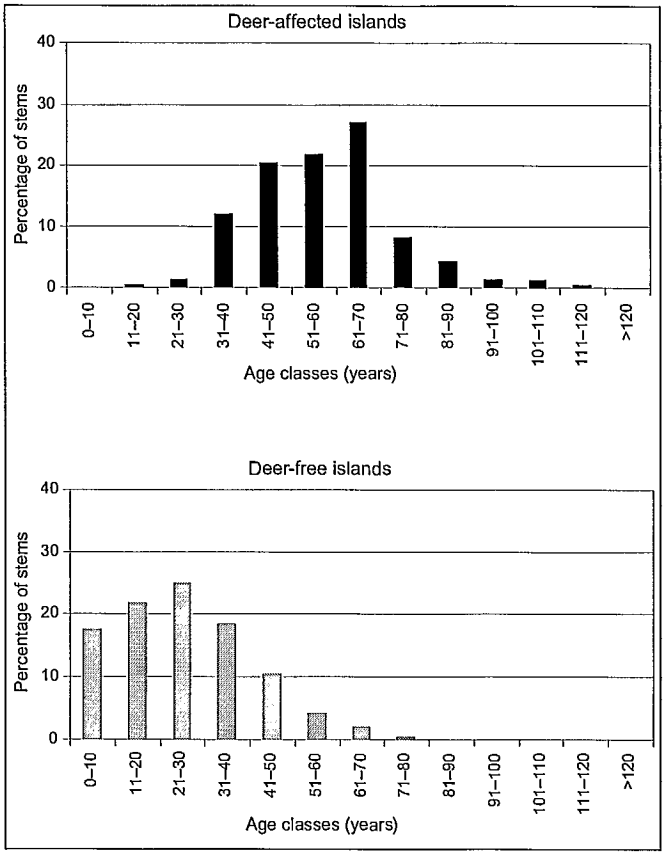
In the absence of written records, the signatures left in woody plants by deer browsing provide several avenues for estimating the local history of deer colonization and abundance (see Pojar this volume, on vegetation changes in historical time; Golumbia et al. this volume).

A first means to assess a minimal date of deer colonization in a locality is to use the cessation of shrub stem recruitment as soon as browsing reaches a certain intensity. This time of cessation of stem recruitment is recorded in the stem age structures (the number of stems per age class), which can be viewed as synthetic indicators of overall level of deer impact and as providing estimates of the time when impact became prevalent at a given locality (Vila et al. 2004b).

On deer-free islands, 93.6% of the stems were less than 50 years old, and at least 15% of the stems belonged to the four youngest age classes (Fig. 7). On deer-affected islands in Laskeek Bay, only 35% of stems were less than 50 years old, and there was a marked deficit of stems in the three or four youngest age classes (Fig. 7). On Louise, Haswell, and Reef islands, the number of stems less than 30 years old was 2%, 0%, and 2.5%, respectively. On Reef Island, only 6.3% of stems were less than 40 years old, while on Louise and Haswell islands, this proportion increased to 14.5% and 14.3%, respectively (Vila et al. 2004b).

These results suggest that deer became prevalent in Laskeek Bay (Louise, Reef, and Haswell islands) at least 40 years before this study. They show that deer impact was most pronounced on Reef Island, where it was prevalent 10 years earlier than on Louise and Haswell islands. However, Reef Island is also the most isolated of the deer-impacted islands we studied and was, therefore, probably colonized last. It has an area of 249 ha and is uniformly covered by forest, whereas Louise Island is much larger and easily accessible from the even larger Moresby Island (Fig. 8). On both Louise and Moresby islands, deer have an easy access to alpine summer range and to clearcuts created by forestry. Haswell Island is only 13.3 ha in size, covered by mature forest, and separated from Louise Island by only a 150-m-wide channel. As the colonization of Reef Island was dependent on the prior colonization of Louise Island and/or Moresby Island, the apparent earlier prevalence of a strong impact of deer suggests that, on Reef Island, it took deer less time to heavily impact the understory vegetation. The causes for that may be an effect of the island's isolation on deer movement, which results in higher population densities (fence effect of Krebs et al. 1969), and/or the lack of easy access on Reef Island to seasonal resources, such as alpine habitats.

Figure 7
Red huckleberry age structures on deer-free and deer-affected islands of the Laskeek Bay area, expressed by the percentage of stems in 10-year age classes

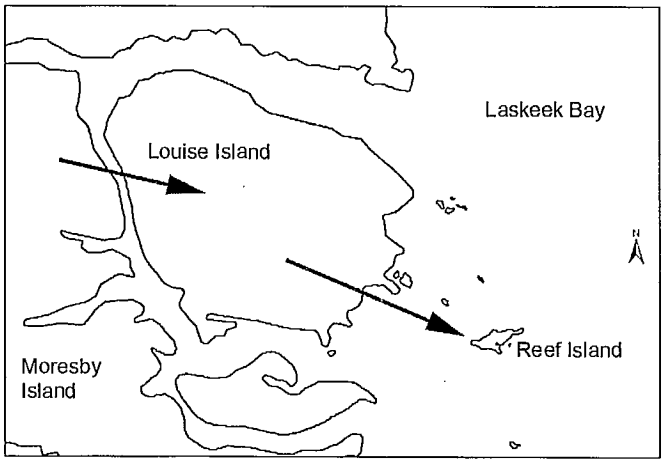


Notwithstanding the magnitude and causes of local variation, the age structure of shrub stems allows, in this situation of relatively recent colonization by the ungulate, an assessment of when the colonizing herbivore began to have a heavy impact in different parts of the archipelago (Vila et al. 2004b, 2005). We could, for instance, show that stem age structures indicate that deer have been the dominant factor structuring the understory for about 40–50 years over a large portion of the southern half of the archipelago (samples from Laskeek Bay, Ramsay Island, and Burnaby Island), with some minor local variation (Vila 2002; Vila et al. 2004b, 2005). There is one notable exception: the south of Moresby Island, where heavy impact on the understory seemed to be not much older than a decade at the time of study, although deer have been present for at least 50 years (Vila et al. 2004b, 2005). An alternative explanation for the longer delay before severe impact may lie with differences in climatic conditions, which can influence deer population dynamics.

In sum, the lack of a progressive north to south gradient in the time of heavy impact of deer on shrub recruitment suggests that the spread of deer across the islands must have been rapid. Exceptions, such as South Skedans Island or the southern end of Moresby Island, on the other hand, suggest that this general pattern can be affected by local peculiarities affecting deer population dynamics.

Because there is a delay between deer arrival and the moment when such changes become apparent in the habitat and because of the local variations just mentioned,

Figure 8
Map of the Laskeek Bay area showing Reef Island isolation and the necessity for the deer to colonize first Louise and/or Moresby islands to reach Reef Island (arrows)



age structures of stems provide a rather conservative estimate of the actual time of colonization of a locality (Vila et al. 2004b). One way to get a more accurate estimation of time of the arrival of deer at a locality is to analyze the age and age distribution of the fraying or bark-stripping scars (Vila et al. 2004a). Fraying scars presumably appear as soon as a population gets established, and the age of the oldest scar can therefore provide a more accurate estimate of the initial colonization of a locality by deer. Scars remain conspicuous for decades. Finally, the time estimate they provide can be compared with the estimate obtained on heavy local impact by the analysis of the age distribution of shrub stems (Vila et al. 2004b). We mostly studied fraying scars in the Laskeek Bay area, comparing them between Reef Island and South Skedans Island. Therefore, we will not be able to provide an archipelago-wide picture of fraying scar distribution. The results obtained show, nevertheless, the potential that rests with such a dendrochronological signature. The age of the oldest scars suggests radical differences between the colonization history of Reef and South Skedans islands. The oldest scar found on South Skedans Island suggests a recent colonization (just before 1987), whereas the oldest scars found on Reef Island suggest that deer colonized Reef Island in the 1940s—an estimate to be compared with the 1960s, estimated as the time of heavy impact by using stem age structure. This more recent age of colonization suggested by dendrochronology for South Skedans Island is consistent with the results obtained for the variation in plant, insect, and bird diversity between different islands (see Allombert and Martin this volume; Martin et al. this volume). Whereas diversity for all three of these components is highest on islands that have never been colonized by deer, it is lowest on islands colonized for at least 50 years, such as Reef Island, and intermediate in South and West Skedans Islands, where colonization, according to dendrochronology, is more recent. Although, in theory, older events of colonization and extinction cannot be excluded, with some recovery of the ecosystem occurring during the periods with no deer, this scenario is not supported by our failure to find older fraying scars on these islands (Vila et al. 2004a).

4.2 Is deer pressure increasing?

Escaped spruce reached the browsing limit 9–12 years ago at about 13 years of age, whereas stunted spruce of the same age at these sites today are still 0.20–0.30 m shorter than the browsing limit. This suggests that browsing pressure increased during the 15 years before our study (Vila et al. 2003a). This could have been caused by an increasing deer density or by a higher browsing pressure on these sites in a context of decreasing forage availability. Under the current growth rate estimates, stunted Sitka spruce are expected to escape at an age of 23 years (Vila 2002).

Age distribution of scars over the 50–60 years before the study for Reef Island and 10–15 years on South Skedans Island shows a constant increase of scar number over the period (Vila et al. 2004a), and the long persistence of the old scars suggests that this increase with time reflects increasing deer pressure. Although site differences in scar densities have often been erroneously analyzed as evidence of density differences, positive relationships between the number of scars and deer population density have been reported for bark-stripping and fraying scars (Gill 1992). In the present study, the pattern of increasing number of fraying scars with time is consistent with the expected increase in deer densities after an initial colonization by deer.

Acknowledgements

We thank all those who worked with us. Special thanks go to Cory Millard, Brian Koepke, Georges Yau, Rob Kelly, and Isabel Buttler for their help in the field and to Mark Salzl, Todd Golumbia, Gwenaël Vourc'h, and Steve Stockton for their scientific help.

Literature cited

Banks, J.C.G. 1991. A review of the use of tree rings for the quantification of forest disturbances. Dendrochronologia 9: 51–70.

Bordage, G.; Filion, L. 1988. Analyse dendroécologique d'un milieu riverain fréquenté par le castor (*Castor canadensis*) au mont du Lac-des-Cygnes (Charlevoix, Québec). Nat. Can. 115: 117–124.

Coates, K.D.; Pollack, J.C.; Barker, J.E. 1985. The effect of deer browsing on the early growth of three conifer species in the Queen Charlotte Islands. Research Report 85002-PR, B.C. Ministry of Forests, Victoria, B.C. 13 pp.

Gill, R.M.A. 1992. A review of damage by mammals in north temperate forests: 1. Deer. Forestry 65(2): 145–169.

Krebs, C.J.; Keller, B.L.; Tamarin, R.H. 1969. *Microtus* population biology: Demographic changes in fluctuating populations of *M. ochrogaster* and *M. pennsylvanicus* in southern Indiana. Ecology 50(4): 587–607.

Martin, J.L.; Baltzinger, C. 2002. Interaction among deer browsing, hunting, and tree regeneration. Can. J. For. Res. 32: 1254–1264.

Martin, J.L.; Daufresne, T. 1999. Introduced species and their impacts on the forest ecosystem of Haida Gwaii. Pages 69–85 *in* G.G. Wiggins (ed.), Proceedings of the cedar symposium: growing western redcedar and yellow-cypress on the Queen Charlotte Islands/Haida Gwaii. B.C. Ministry of Forests/ Canada–British Columbia South Moresby Forest Replacement Account, Victoria, B.C.

Morneau, C.; Payette, S. 1998. A dendroecological method to evaluate past caribou (*Rangifer tarandus* L.) activity. Ecoscience 5(1): 64–70.

Morneau, C.; Payette, S. 2000. Long-term fluctuations of a caribou population revealed by tree-ring data. Can. J. Zool. 78: 1784–1790.

Motta, R. 1995. Dendroecology in ungulate forest damages: 1. Fraying scars. Dendrochronologia 13: 33–41.

Motta, R. 1996. Impact of wild ungulates on forest regeneration and tree composition of mountain forests in the Western Italian Alps. For. Ecol. Manage. 88: 93–98.

Motta, R. 1997. Dendroecology in ungulate forest damage: 2. Bark stripping scars. Dendrochronologia 15: 11–22.

Payette, S. 1987. Recent porcupine expansion at tree line: a dendroecological analysis. Can. J. Zool. 65: 551–557.

Pojar, J.; Banner, A. 1984. Old-growth forests and introduced black-tailed deer on the Queen Charlotte Islands, British Columbia. Pages 247–257 in W.R. Meehan, T.R. Merrell, Jr., and T.A. Hanley (eds.), Fish and wildlife relationships in old-growth forests: Proceedings of a symposium held in Juneau, Alaska, 12–15 April 1982. American Institute of Fishery Research Biologists, Morehead City, North Carolina.

Pojar, J.; Lewis, T.; Roemer, H.; Wildford, D.J. 1980. Relationships between introduced black-tailed deer and the plant life of the Queen Charlotte Islands, British Columbia. Unpublished report, B.C. Ministry of Forests, Smithers, B.C.

Schweingruber, F.H. 1988. Tree-rings, basics and applications of dendrochronology. D. Reidel Publishing Company, Dordrecht, Netherlands. 276 pp.

Schweingruber, F.H. 1996. Tree rings and environment. Dendroecology. Swiss Federal Institute for Forest, Snow and Landscape Research, Birmensdorf. Paul Haupt, Berne, Stuttgart. 609 pp.

Vila, B. 2002. [Influence of a large browsing mammal on forest dynamics—a dendrochronological study of present and past impact of introduced black-tailed deer on vegetation in Haida Gwaii islands (Canada).] Ph.D. thesis, University of Aix-Marseille III, Marseille, France. 81 pp. + annexes (in French).

Vila, B.; Keller, T.; Guibal, F. 2001. Influence of browsing cessation on *Picea sitchensis* radial growth. Ann. For. Sci. 58: 853–859.

Vila, B.; Vourc'h, G.; Martin, J.-L.; Guibal, F. 2002. Is escaping deer browse just a matter of time in *Picea sitchensis*? A chemical and dendroecological approach. Trees – Struct. Funct. 16: 488–496.

Vila, B.; Guibal, F.; Martin, J.-L.; Torre, F. 2003a. Growth change of young *Picea sitchensis* in response to deer browsing. For. Ecol. Manage. 180: 413–424.

Vila, B.; Torre, F.; Martin, J.-L.; Guibal, F. 2003b. Response of young *Tsuga heterophylla* to deer browsing: developing tools to assess deer impact on forest dynamics. Trees – Struct. Funct. 17: 547–553.

Vila, B.; Guibal, F.; Torre, F.; Martin, J.-L. 2004a. Assessing spatial variation in browsing history by means of fraying scars. J. Biogeogr. 31: 987–995.

Vila, B.; Martin, J.-L.; Guibal, F.; Torre, F. 2004b. Can we reconstruct browsing history and how far back? Lessons from *Vaccinium parvifolium* Smith in Rees. For. Ecol. Manage. 201: 171–185.

Vila, B.; Guibal, F.; Torre, F.; Martin, J.-L. 2005. Can we reconstruct deer browsing history and how? Lessons from *Gaultheria shallon* Pursh. Ann. For. Sci. 62: 153–162.

Vourc'h, G.; Vila, B.; Gillon, D.; Escarré, J.; Guibal, F.; Fritz, H.; Clausen, T.P.; Martin, J.-L. 2002. Disentangling the causes of damage variation by deer browsing on young *Thuja plicata*. Oikos 98: 271–283.

The effects of deer on plant diversity

Stephen A. Stockton

Abstract

We examined the effects of deer on the cover and diversity of understory plants utilizing an unplanned natural experiment, the introduction of Sitka black-tailed deer *Odocoileus hemionus sitkensis* Merriam to Haida Gwaii (Queen Charlotte Islands, British Columbia) in the late 19th century. The absence of wolves *Canis lupus* L. and cougars *Puma concolor* L., coupled with the mild winter conditions that occur in this archipelago, leave these deer without external population constraints, effectively isolating the relationship between plant and herbivore. We measured the cover of vegetation and the number of vascular plant species occurring in 105 circular plots of 10-m radius on a series of seven islands: two affected by deer for more than 50 years, two affected by deer for less than 20 years, and three with no history of deer presence. Within this set of islands, both cover of vegetation and plant diversity declined with increased duration of deer presence. Our results demonstrate that predator-free deer populations have the capacity to greatly alter understory vegetation.

1. Introduction

Deer populations, unregulated by natural predators, have become a major factor controlling forest ecosystem dynamics in many parts of North America (Sullivan et al. 1990; Diamond 1992) and Europe (Hester et al. 1991; Baines et al. 1994; Gill 1999). As deer overabundance becomes evident (McShea et al. 1997), a clear understanding of the long-term consequences for plant diversity becomes increasingly important.

Many studies have demonstrated the effects of high population densities of white-tailed deer *Odocoileus virginianus* on the vegetation of the eastern hardwood forests of North America (see Waller this volume). White-tailed deer have been implicated in the reduced abundance and diversity (Frelich and Lorimer 1985; Alverson et al. 1988; Tilghman 1989; deCalesta 1997a,b; Waller and Alverson 1997; McShea and Rappole 2000) and in some instances the extirpation of woody plant species from these forests (Hough 1965; Whitney 1984; Rooney and Dress 1997a). They have been associated with a shift in plant community composition from shrubs and herbs to grasses and ferns (Horsley and Marquis 1983) and the reduced frequency of many plant species listed as threatened or endangered (Miller et al. 1992; Anderson 1994; Rooney and Dress 1997a; Augustine and Frelich 1998). In contrast, only a handful of studies have examined the effects of mule deer *Odocoileus hemionus* or black-tailed deer *Odocoileus hemionus* sspp. on the plant communities of the temperate rainforest of North America (Klein 1965; Banner et al. 1989; Woodward et al. 1994; Daufresne and Martin 1997; Wiggins 1999). Hence, the deliberate introduction of deer to Haida Gwaii (Queen Charlotte Islands, British Columbia) in the late 19th century (Osgood 1901; Munro 1935; Golumbia et al. this volume) provides a valuable opportunity to study an unusually clear example of the potential of Sitka black-tailed deer *Odocoileus hemionus sitkensis* to modify forest vegetation.

2. Methods

The seven islands included in our study—Haswell, West Limestone, West Skedans, South Skedans, Low, South Low, and Lost—were selected to control for island area and to include islands with different durations of deer presence (for details, see Stockton and Gaston this volume).

We obtained estimates of the duration of deer presence on the different islands in Laskeek Bay (Table 1 in Stockton and Gaston this volume) from comparative analyses of shrub stem age structures and the dating of fraying scars (Vila 2002). South Low, Low, and Lost islands showed no sign of deer, past or present. West and South Skedans islands showed evidence of deer for less than 20 years. West Limestone and Haswell islands showed evidence of deer presence for more than 50 years.

We recognized two distinct habitat types on these islands: the forest edge and the forest interior. Small islands such as these inherently possess a high edge-to-interior ratio, the edge being heavily influenced by wind and salt spray (Calder and Taylor 1968). As such, we sampled each island with 10 randomly spaced 10-m-radius circular plots along the forest edge and five randomly placed 10-m-radius circular plots within the forest interior, sampling 3–10% of each island. Species were identified according to Pojar and MacKinnon (1994) and verified with Hitchcock and Cronquist (1991).

The percent cover of each vascular plant species as well as the total cover of vegetation in each of five strata were estimated using standard spot charts (Mueller-Dombois

and Ellenberg 1974) by the same two observers. The strata were set at heights of 0–0.5, 0.5–1.5, 1.5–4, 4–8, and >8 m. These were chosen to highlight the effects of the deer, which are known to feed primarily upon vegetation below 1.5 m (Martin and Daufresne 1999), and to capture and compare different elements of plant communities.

A Type 1 ANOVA was used to determine differences in covers and species among the seven islands. Post hoc Tukey HSD (Spjotvoll/Stoline) tests (Sokal and Rohlf 1995) were performed to compare the differences in these measures between individual islands.

3. Results

Vegetation cover differed significantly among the seven islands in all strata, both in the interior (Figs. 1–5) and along the forest edge (Figs. 6–8). In the lower strata (below 1.5 m), plots on islands with deer showed lower average cover than plots on islands without deer in all cases (significant in all but one case). On South Skedans Island (with <20 years of deer presence), the average cover below 0.5 m of plots in the forest interior was not significantly different from that of Lost, Low, and South Low islands (all with no deer). Upper strata (above 1.5 m) showed patterns inconsistent with the presence of deer, except for the 1.5- to 4-m stratum in the interior, which again showed lower average cover on islands with deer.

Average cover per plot in the forest interior (Figs. 1–5) showed large stepwise reduction with longer deer presence from 0 to 0.5 m, 0.5 to 1.5 m, and 1.5 to 4 m. Cover at 0.5–1.5 m and 1.5–4 m on West Skedans and South Skedans islands (both with <20 years of deer presence) showed much variation among plots, which supported either a dense cover of salal *Gaultheria shallon* or virtually no cover at all. Reduced cover between 1.5 and 4 m, beyond the immediate reach of the deer, appeared to be caused by deer pushing over and defoliating shrubs with flexible stems, behaviour that was observed on several occasions. From

Figure 1
Vegetation cover in the 0- to 0.5-m layer of forest interior 10-m plots: open columns, unbrowsed; shaded columns, with deer present for less than 20 years; black columns, with deer present for more than 50 years. Values labelled with the same letter do not differ significantly in post hoc Tukey HSD (Spjotvoll/Stoline) tests ($P > 0.05$).

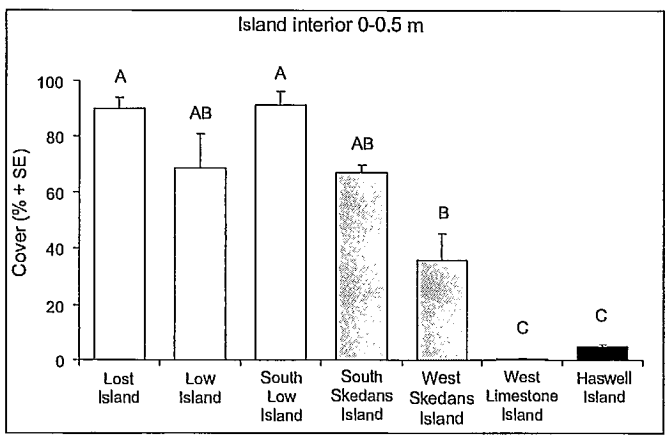


Figure 2
Vegetation cover in the 0.5- to 1.5-m layer of forest interior plots: conventions as for Figure 1

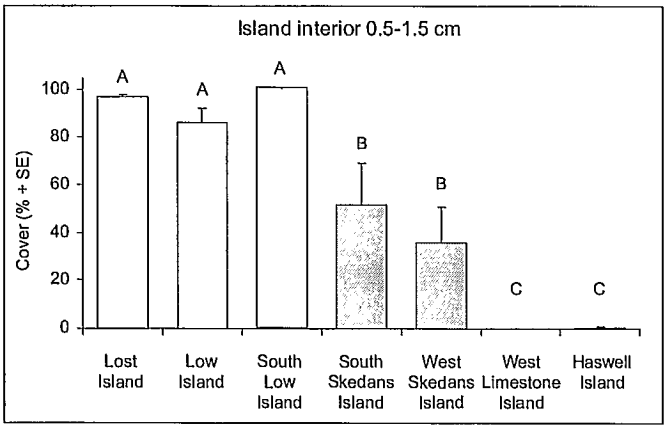


Figure 3
Vegetation cover in the 1.5- to 4-m layer of forest interior plots: conventions as for Figure 1

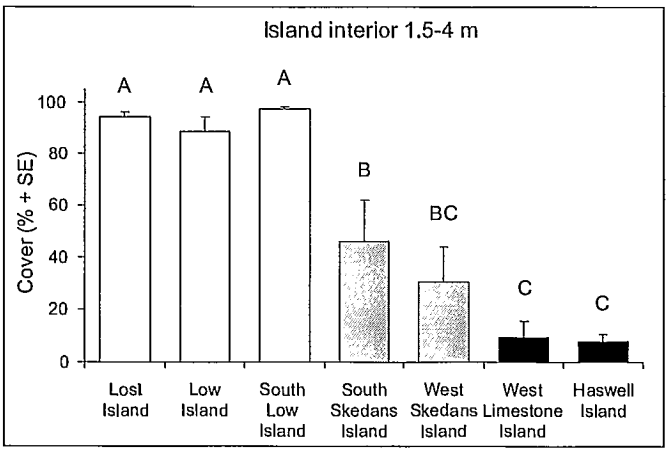


Figure 4
Vegetation cover in the 4- to 8-m layer of forest interior plots: conventions as for Figure 1

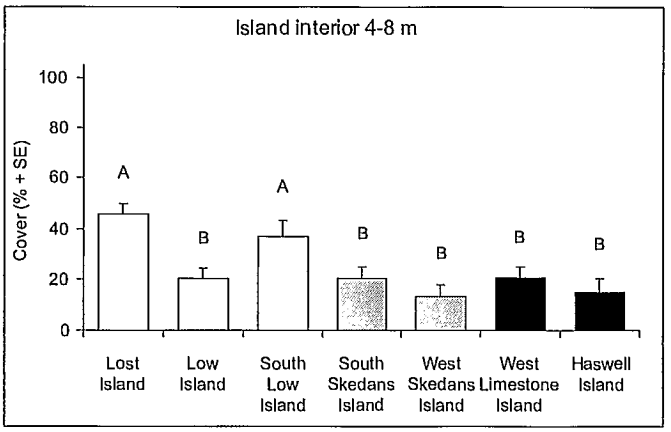


Figure 5
Vegetation cover in the >8-m layer of forest interior plots: conventions as for Figure 1

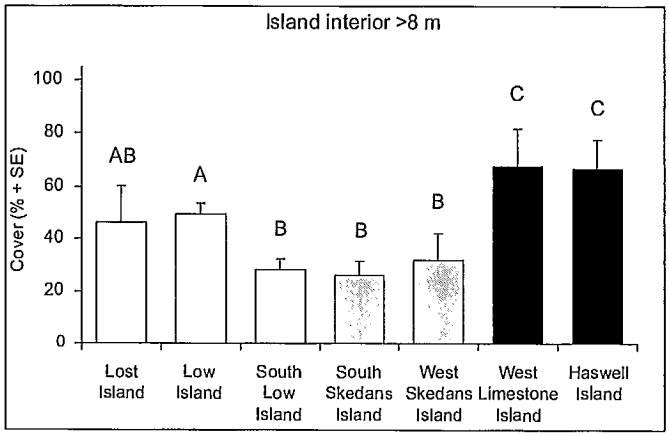
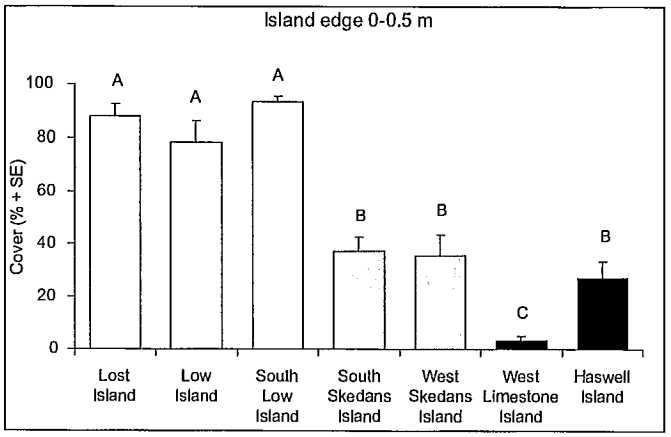


Figure 6
Vegetation cover in the 0- to 0.5-m layer of forest edge plots: conventions as for Figure 1



4 to 8 m, the average cover per plot in the interior of Lost and South Low islands (made up largely of salmonberry *Rubus spectabilis* and/or thimbleberry *Rubus parviflorus*) was significantly higher than on all other islands. Cover above 8 m in the interior of West Limestone and Haswell islands (both with >50 years of deer presence) showed large variation between plots but was on average significantly greater than that of the other five islands.

Average cover along the forest edge (Figs. 6–8) was greatly reduced on all islands with deer from 0 to 0.5 m and 0.5 to 1.5 m. Cover below 0.5 m on Haswell Island was largely made up of plants that persisted within a thick moss layer. Between 1.5 and 4 m, cover on all islands was made up predominately of stunted Sitka spruce *Picea sitchensis*. The average cover on South Low Island (complemented by an abundance of tall dunegrass *Elymus mollis* and fireweed *Epilobium angustifolium*) was greater than on the other six islands, which were largely similar in cover. No cover was recorded above 4 m along the forest edge on any island.

The average number of species recorded per plot differed significantly among the seven islands, both along the forest edge (Fig. 9) and in the interior (Fig. 10). In all cases, fewer species per plot were found on islands with deer than on islands without deer. Along the forest edge, this difference was significant in all cases. In the interior, Lost and South Low islands averaged significantly more species per plot than South Skedans and West Limestone islands. The average number of species per plot in the interior of Low, West Skedans, and Haswell islands was intermediate between these two pairs.

4. Discussion

Our study demonstrates that unregulated Sitka black-tailed deer populations have had strong effects on the abundance and diversity of the vegetation in our study area. Plots on islands affected by deer showed significantly less vegetation cover and a significantly lower diversity than those without deer. The difference in the vegetation on islands with and without deer was often extreme, ranging from dense, lush, sometimes impenetrable vegetation on

Figure 7
Vegetation cover in the 0.5- to 1.5-m layer of forest edge plots: conventions as for Figure 1

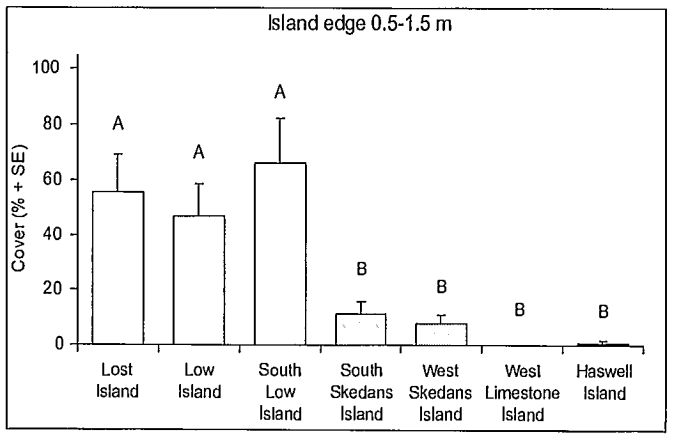


Figure 8
Vegetation cover in the 1.5- to 4-m layer of forest edge plots: conventions as for Figure 1

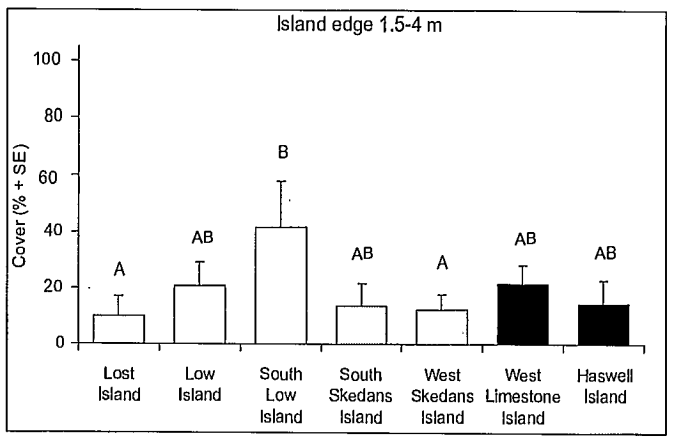


Figure 9
Species richness (mean number of species per 10-m-radius circular plot) in forest edge plots: conventions as for Figure 1

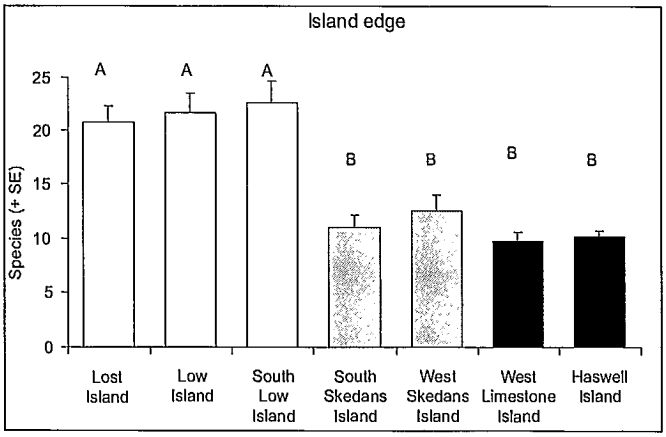
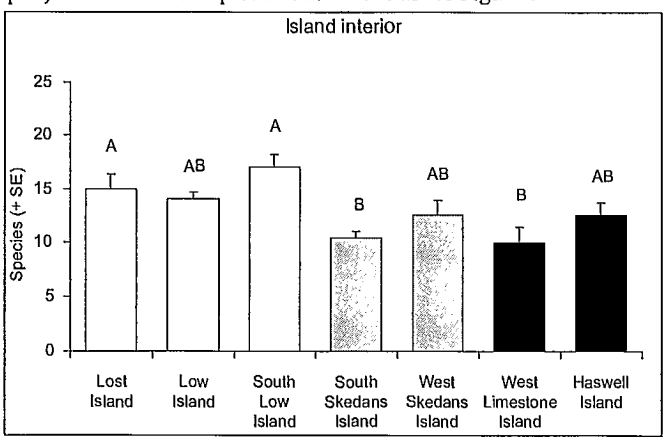


Figure 10
Species richness (mean number of species per 10-m-radius circular plot) in forest interior plots: conventions as for Figure 1



islands free of deer to barren areas where only a few stunted individual plants remained on the most heavily browsed islands.

Cover of vegetation in the forest interior showed large stepwise reduction with increased duration of deer presence (Figs. 1–5), demonstrating the powerful force of modification that can be exerted through deer herbivory. The diverse array of ferns and shrubs, which occurred in abundance in the understory of islands without deer, was reduced on islands with deer for less than 20 years to a series of remnant patches consisting mostly of salal. On islands with deer for more than 50 years, vegetation in the understory was virtually eliminated. Although abundant foliage persisted beyond the reach of the deer, deer had pushed over and defoliated many shrubs above their immediate reach. By eliminating the vegetation within their reach, deer may also have affected recruitment to upper levels of the forest (Vila et al. 2001). Deer are known to affect even long-lived canopy species by reducing or eliminating recruitment (Anderson and Loucks 1979; Alverson et al. 1988; Anderson and Katz 1993).

Modification of the vegetation at the forest edge by deer was also clearly demonstrated. Cover of vegetation along the forest edge was reduced with increased deer duration (Figs. 6–8). Although the deep moss layer on Haswell Island appeared to offer limited refuge for some vascular plants, vegetation was virtually eliminated between this layer and the foliage of stunted conifers above 1.5 m.

Dense canopy cover (above 8 m; Fig. 5) in interior plots on Haswell and West Limestone islands may have contributed to the large difference in the cover in these plots relative to those of other islands; however, the effect appears quite small. Although large variation occurred in the vegetation above 8 m in interior plots on Haswell and West Limestone islands, the understory in these plots was uniformly empty, even in those plots with relatively little canopy cover. In contrast, the understory in plots on islands without deer was uniformly dense regardless of canopy cover. Forest edge plots (Figs. 6 and 7) without the effects of canopy closure (these possessed no vegetation above 4 m) showed similar reductions in cover with deer. The effects of canopy cover within the small islands of Laskeek Bay appeared far less important than the effects of deer in determining the cover of understory vegetation.

Three patterns demonstrate that the difference in vegetation between islands is largely the effect of deer modification. Firstly, on islands affected by deer, in difficult to access areas, such as steep cliffs, the tops of rock stacks, stumps, and suspended logs, we observed a lush and rich variety of vegetation, paralleling that found on islands without deer. A similar deer browse signature has been recorded for sensitive forbs in eastern forests (Rooney 1997). Secondly, Sitka black-tailed deer are known to feed primarily on vegetation below 1.5 m (Martin and Daufresne 1999). Thus, the pattern of reduced vegetation principally below this level is a clear indication of the predominant role that deer have played in shaping the current vegetation structure on the islands they have colonized. Thirdly, the sparse understory that occurs today over much of Haida Gwaii (Calder and Taylor 1968; Banner et al. 1989; Pojar 1999) contrasts greatly with the consistently dense understory noted by early foresters and visitors (Gregg 1923; Hopkinson 1931; Hall 1937; Carr 1951). This suggests that major changes to the vegetation of this archipelago have occurred quite recently, contemporary with the spread of deer.

A modification of this magnitude is likely to influence ecosystem processes such as nutrient cycling and disturbance regimes (Hobbs 1996), as well as reduce the quantity of habitat and resources available in the food chain. A decrease in the abundance of songbirds and insects on islands affected by deer has been shown within Laskeek Bay (Martin, Allombert, and Gaston this volume; Allombert and Martin this volume). Similar decreases in the abundance and diversity of bird communities through the modification of forest vegetation have been shown in eastern North America (deCalesta 1997b). Reduced faunal diversity could potentially further diminish the viability of remaining plants through pollinator reduction or the absence of appropriate seed vectors. Reduced pollination has been found on several tropical islands subject to introduced herbivore species (Cox and Elmqvist 2000). The arrival of deer in Haida Gwaii may

have initiated a vortex of ecosystem dislocation, reducing the viability and productivity of all forest components.

The deleterious effects of deer apparent in our study generally agree with the results of previous studies of the impact of black-tailed deer on forest understory communities (Klein 1965; Woodward et al. 1994; Daufresne and Martin 1997) and the impact of other deer species on forest vegetation (Alverson et al. 1988; Anderson and Katz 1993; deCalesta 1997b); these studies all recorded a decreased plant abundance and/or plant species richness in the presence of moderate to high deer densities. However, in Laskeek Bay, the effect of deer has been more acute than that recorded by most mainland deer studies (Alverson et al. 1988; Woodward et al. 1994; deCalesta 1997b). Mainland studies have usually occurred in contexts where several other factors (forest industry, agriculture, and urban development) may have played a role in the emerging pattern. The study of areas with minimal external factors indicates that large differences in cover and diversity may be the effect of deer alone (Rooney and Dress 1997b). The absence of other human-driven factors affecting the interaction of deer with the forest in Laskeek Bay makes the results of our study especially valuable in determining the precise role of deer in ecosystem modification.

5. Conclusion

Our investigation suggests that in the absence of predators or where predator pressure is severely reduced, deer have a strong impact on vegetation cover and plant diversity. The possible cascading effects of deer browsing on plant–plant and plant–animal interactions may have far-reaching impacts on the flora and fauna of one of the largest remaining tracts of coastal temperate rainforest. Moreover, as many of these species are culturally significant for the Haida (Turner 1995, 1998), modification of the flora and fauna of this region has direct cultural impacts. Of special note, in this context, is the extremely high conservation value of the remaining islands in Haida Gwaii without deer. Small remote islands, such as Low, South Low, and Lost islands, may provide refuge for rare or endemic species sensitive to the effects of deer browse. Preservation of these island refuges may be critical in maintaining the biodiversity of this region and may provide valuable seed stores for future restoration efforts. In addition, at a broader geographic scale, our results emphasize that the careful maintenance of predator populations and other deer population control mechanisms, where they exist in the temperate rainforest, should be a conservation priority.

6. Acknowledgements

This study would not have been possible without the guidance of Tony Gaston and Jean-Louis Martin. I am greatly indebted to both of them for their continued wisdom and patience. I have been greatly blessed to work with such a talented and ingenious team as the Research Group on Introduced Species, especially Liann Bobechko, who kept me on track and made all the rainy days sunny.

Literature cited

Alverson, W.S.; Waller, D.M.; Solheim, S.L. 1988. Forests too deer: edge effects in northern Wisconsin. Conserv. Biol. 2: 348–358.

Anderson, R.C. 1994. Height of white-flowered trillium *Trillium grandiflorum* as an index of deer browsing intensity. Ecol. Appl. 4: 104–109.

Anderson, R.C.; Katz, A.J. 1993. Recovery of browse-sensitive tree species following release from white-tailed deer *Odocoileus virginianus* Zimmerman browsing pressure. Biol. Conserv. 63: 203–208.

Anderson, R.C.; Loucks, O.L. 1979. White-tailed deer *Odocoileus virginianus* influence on structure and composition of *Tsuga canadensis* forests. J. Appl. Ecol. 16: 855–861.

Augustine, D.J.; Frelich, L.E. 1998. Effects of white-tailed deer on populations of an understory forb in fragmented deciduous forests. Conserv. Biol. 12: 995–1004.

Baines, D.; Sage, R.B.; Baines, M.M. 1994. The implications of red deer grazing to ground vegetation and invertebrate communities of Scottish native pinewoods. J. Appl. Ecol. 31: 776–783.

Banner, A.; Pojar, J.; Schwab, J.W.; Trowbridge, R. 1989. Vegetation and soils of the Queen Charlotte Islands: recent impacts of development. Pages 261–279 *in* G.G.E. Scudder and N. Gessler (eds.), The outer shores. Queen Charlotte Islands Museum Press, Skidegate, B.C.

Calder, J.A.; Taylor, R.L. 1968. Flora of the Queen Charlotte Islands. Part 1. Systematics of the vascular plants. Monograph 4, Research Branch, Department of Agriculture, Ottawa, Ontario.

Carr, E. 1951. Klee Wyck. Clarke Irwin, Toronto.

Cox, P.A.; Elmqvist, T. 2000. Pollinator extinction in the Pacific islands. Conserv. Biol. 14: 1237–1239.

Daufresne, T.; Martin, J.-L. 1997. Changes in vegetation structure and diversity in relation to the presence of a large herbivore: the impact of introduced black-tailed deer on the old-growth forests in Haida Gwaii. Pages 2–26 *in* A.J. Gaston (ed.), Laskeek Bay Research 7. Laskeek Bay Conservation Society, Queen Charlotte City, B.C.

deCalesta, D.S. 1997a. Ecosystem management for deer. Pages 267–279 *in* W.J. McShea, J.H. Rappole, and H.B. Underwood (eds.), The science of overabundance: deer ecology and population management. Smithsonian Institution, Washington, D.C.

deCalesta, D.S. 1997b. Deer, ecosystem damage, and sustaining forest resources. *In* Deer as public goods and public nuisances—Issues and policy options in Maryland: Proceedings of a conference. Center for Agricultural and Natural Resource Policy, University of Maryland, College Park, Maryland. Available at http://www.arec.umd.edu/Policycenter/Deer-Management-in-Maryland/decalesta.htm.

Diamond, J.M. 1992. Must we shoot deer to save nature? Nat. Hist. 8: 2–8.

Frelich, L.E.; Lorimer, C.G. 1985. Current and predicted long-term effects of browsing on hemlock forests in Michigan, U.S.A. Biol. Conserv. 34: 99–120.

Gill, R. 1999. Deer management to protect forest vegetation, a British perspective. Pages 59–68 *in* G.G. Wiggins (ed.), Proceedings of the cedar symposium: growing western redcedar and yellow-cypress on the Queen Charlotte Islands/Haida Gwaii. B.C. Ministry of Forests/Canada–British Columbia South Moresby Forest Replacement Account, Victoria, B.C.

Gregg, E.E. 1923. Cruise on Queen Charlotte Islands. Unpublished report, B.C. Forest Service, Victoria, B.C.

Hall, W. 1937. Moresby Forest: Survey and preliminary management plan. Unpublished report, B.C. Forest Service, Victoria, B.C.

Hester, A.J.; Miles, J.; Gimmingham, C.H. 1991. Succession from heather moorland to birchwood. 1: Experimental alteration of specific environmental conditions in the field. J. Ecol. 79: 303–315.

Hitchcock, C.L.; Cronquist, A. 1991. Flora of the Pacific Northwest. University of Washington Press, Seattle, Washington.

Hobbs, N.T. 1996. Modification of ecosystems by ungulates. J. Wildl. Manage. 60: 695–713.

Hopkinson, A.D. 1931. A visit to Queen Charlotte Islands. Empire For. 10: 20–36.

Horsley, S.B.; Marquis, D.A. 1983. Interference by weeds and deer with Allegheny hardwood reproduction. Can. J. For. Res. 13: 61–69.

Hough, A.F. 1965. A twenty-year record of vegetation change in a virgin Pennsylvania forest. Ecology 46: 370–373.

Klein, D.R. 1965. Ecology of deer range in Alaska. Ecol. Monogr. 35: 259–284.

Martin, J.-L.; Daufresne, T. 1999. Introduced species and their impacts on the forest ecosystem of Haida Gwaii. Pages 69–85 *in* G.G. Wiggins (ed.), Proceedings of the cedar symposium: growing western redcedar and yellow-cypress on the Queen Charlotte Islands/Haida Gwaii. B.C. Ministry of Forests/ Canada–British Columbia South Moresby Forest Replacement Account, Victoria, B.C.

McShea, W.J.; Rappole, J.H. 2000. Managing the abundance and diversity of breeding bird populations through manipulation of deer populations. Conserv. Biol. 14: 1161–1170.

McShea, W.J.; Underwood, H.B.; Rappole, J.H. (eds.). 1997. The science of overabundance: deer ecology and population management. Smithsonian Institution, Washington, D.C.

Miller, S.G.; Bratton, S.P.; Hadidan, J. 1992. Impacts of white-tailed deer on endangered and threatened vascular plants. Nat. Areas J. 12: 67–75.

Mueller-Dombois, D.; Ellenberg, H. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York.

Munro, J.A. 1935. The introduction of coast deer and ring-necked pheasant on Graham Island, British Columbia. B.C. Game Commission, Victoria, B.C.

Osgood, W.H. 1901. Natural history of the Queen Charlotte Islands, British Columbia. North American Fauna No. 21, Government Printing Office, Washington, D.C. 87 pp.

Pojar, J. 1999. The effects of deer browsing on the plant life of Haida Gwaii. Pages 90–97 *in* G.G. Wiggins (ed.), Proceedings of the cedar symposium: growing western redcedar and yellow-cypress on the Queen Charlotte Islands/Haida Gwaii. B.C. Ministry of Forests/Canada–British Columbia South Moresby Forest Replacement Account, Victoria, B.C.

Pojar, J.; MacKinnon, A. 1994. Plants of coastal British Columbia, including Washington, Oregon and Alaska. Lone Pine Publishing, Vancouver, B.C.

Rooney, T.P. 1997. Escaping herbivory: refuge effects on the morphology and shoot demography of the clonal forest herb, *Maianthemum canadense*. Bull. Torrey Bot. Club 124: 280–285.

Rooney, T.P.; Dress, W.J. 1997a. Species loss over sixty-six years in the ground layer of Heart's Content, an old growth forest in Pennsylvania. Nat. Areas J. 17: 297–305.

Rooney, T.P.; Dress, W.J. 1997b. Patterns of plant diversity in overbrowsed old growth and mature second growth hemlock–northern hardwood forest stands. J. Torrey Bot. Soc. 124: 3–51.

Sokal, R.R.; Rohlf, F.J. 1995. Biometry: the principles and practice of statistics in biological research. 3rd ed. W.H. Freeman, New York.

Sullivan, T.P.; Harestad, A.S.; Wilkeem, B.M. 1990. Control of mammal damage. Pages 8–34 *in* D.P. Lavender, R. Parish, C.M. Johnson, G. Montgomery, A. Vyse, R.A. Willis, and D. Winston (eds.), Regenerating British Columbia forests. University of British Columbia Press, Vancouver, B.C.

Tilghman, N.G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. J. Wildl. Manage. 53: 524–532.

Turner, N.J. 1995. Food plants of coastal First Peoples. University of British Columbia Press, Vancouver, B.C.

Turner, N.J. 1998. Plant technology of First Peoples in British Columbia. University of British Columbia Press, Vancouver, B.C.

Vila, B. 2002. [Influence of a large browsing mammal on forest dynamics—a dendrochronological study of present and past impact of introduced black-tailed deer on vegetation in Haida Gwaii islands (Canada).] Ph.D. thesis, University of Aix-Marseille III, Marseille, France. 81 pp. + annexes (in French).

Vila, B.; Guibal, F.; Martin, J.-L. 2001. Impact of browsing on forest in Haida Gwaii: a dendro-ecological approach. Pages 62–73 *in* A.J. Gaston (ed.), Laskeek Bay Research 10. Laskeek Bay Conservation Society, Queen Charlotte City, B.C.

Waller, D.M.; Alverson, W.S. 1997. The white-tailed deer: a keystone herbivore. Wildl. Soc. Bull. 25: 217–226.

Whitney, G.G. 1984. Fifty years of change in the arboreal vegetation of Heart's Content, an old growth hemlock – white pine – northern hardwood stand. Ecology 65: 403–408.

Wiggins, G.G. (ed.). 1999. Proceedings of the cedar symposium: growing western redcedar and yellow-cypress on the Queen Charlotte Islands/Haida Gwaii. B.C. Ministry of Forests/ Canada–British Columbia South Moresby Forest Replacement Account, Victoria, B.C.

Woodward, A.; Schreiner, E.G.; Houston, D.B.; Moorhead, B.B. 1994. Ungulate–forest relationships in Olympic National Park: retrospective exclosure studies. Northwest Sci. 68: 97–110.

Interaction between Sitka black-tailed deer and western redcedar: Lessons from Haida Gwaii

Gwenaël Vourc'h, José Escarré, and Jean-Louis Martin

Abstract

The archipelago of Haida Gwaii (Queen Charlotte Islands, British Columbia) is covered by a temperate rain forest and evolved without large herbivore browsers after the last glaciation (10 000 years BP) until Sitka black-tailed deer *Odocoileus hemionus sitkensis* were introduced in the late 19th century. This quasi-experimental situation allowed us to study how herbivory by a large mammal, the Sitka black-tailed deer, influences defence traits of a long-lived plant, the western redcedar *Thuja plicata*. We showed that monoterpenes are one of the keys determining food choice by black-tailed deer on redcedar, whereas diterpenes and nutritive compound content do not account for variation in browsing. Using the absence of herbivore browsers on Haida Gwaii, we investigated the existence of cost of defences by testing whether Haida Gwaii redcedars were less defended than mainland ones. We found that the proportion of trees with low levels of chemical defences increased in the western redcedar population of Haida Gwaii, which suggests a low defence cost. Finally, using the deer introduction on Haida Gwaii as well as defence variation on juvenile redcedars in common garden experiments, our results suggested that herbivory pressure by deer can select for redcedars that are most defended where redcedar regeneration is possible and abundant enough.

1. Introduction

Those who have had the chance to visit the few deer-free islands of Haida Gwaii (Queen Charlotte Islands, British Columbia) have been able to admire the abundance and thickness of their understory compared with the open old-growth understory on islands with deer. What is further intriguing is that the understory on the islands with deer appears even more barren than the understory of forests in areas with high deer populations on the British Columbia mainland. Has this something to do with specifics of the plant populations growing on Haida Gwaii?

Plant defences are traits that decrease plant consumption by herbivores. These traits can be physical, such as spines or thorns, or chemical, such as terpenes. These traits can at the same time have functions other than defence. Terpenes, for example, play a role against herbivores (Paré and Tumlinson 1999; Phillips and Croteau 1999) and also in protecting plants against high temperatures (Sharkey and Yeh 2001; Peñuelas and Llusià 2002). In turn, herbivores have developed adaptations to counter these defences (Simms 1990; Robbins et al. 1995; Hanley 1997). After ingesting the plant, herbivores can metabolize and degrade the chemical compounds or excrete them. In addition, herbivores can choose to eat plants that are the least defended, thanks to stimuli such as odours. Chemical defences vary among species: e.g., oak (*Quercus* sp.) leaves have high tannin concentrations, whereas some foxgloves (*Digitalis* spp.) have cardiotonic glycosides. They also vary among populations within a species (cyanogenic and acyanogenic morphs of white clover *Trifolium repens*; Dirzo and Harper 1982), as well as within an individual as a result of developmental stage or its recent history of herbivory. Variation of plant defences with age may result from developmental constraints or from stronger selection for defence against herbivores and pathogens at the juvenile, rather than the adult, stage (Bryant and Julkunen-Tiitto 1995; Fritz et al. 2001; Swihart and Bryant 2001). In addition, after browsing, the nutritional quality of a plant may increase through changes in the carbon–nitrogen ratio (Chapin et al. 1985) or decrease as a result of the induction of chemical defences (Tallamy and Raupp 1991; Karban and Baldwin 1997; Agrawal and Karban 1999).

In studying variation in plant chemical defences, we need to consider (e.g., Rhoades and Cates 1976; Coley 1986; Simms 1992) 1) the benefits of defences to the plants (reduced consumption of plants with high defences), 2) their costs in terms of the energy used to produce defences, assuming that it cannot be allocated elsewhere (e.g., reproduction or growth), and 3) the genetic or metabolic constraints in the production of defences.

Experimental and theoretical work on the defence of plants against herbivores has mostly involved short-lived plants (generally herbaceous) and/or invertebrate herbivores (e.g., Berenbaum et al. 1986; Marquis 1992; Mauricio and Rausher 1997; Elle et al. 1999). Thanks to their short generation time, these biological models are relatively easier to use than long-lived plants. Studies with long-lived plants and large herbivores are comparatively few (Danell et al. 1985; Palo and Robbins 1991; Bryant et al. 1992; Snyder and Linhart 1998), but nevertheless crucial, because long-lived plants are a major component of the terrestrial biomass. Mammalian herbivores are the main herbivores in temperate

and polar ecosystems, especially in winter, when invertebrate herbivores are absent or inactive (Swihart and Bryant 2001). Another point of interest is that generally long-lived plants interact, during their lifetime, with several herbivore species and several generations of herbivores (Wallin and Raffa 2001), the effect of the herbivore varying with the developmental stage of the plant (Pollard 1992). A small seedling is much more vulnerable to deer than a 60-m-high tree. The difficulties in studying this interaction are the time and space required for the experiments, as well as the difficulty in producing fitness estimates, which are central to evolutionary biology (Barbosa and Schultz 1987).

The temperate climate of British Columbia and the nature of its forests, dominated by a few long-lived conifers and a limited number of large herbivore species, provide an ideal natural system to investigate the interaction between large herbivores and long-lived plants. The introduction, at the end of the 19th century, of the Sitka black-tailed deer *Odocoileus hemionus sitkensis* Merriam, the main deer species in these forests on the mainland, to the forests of Haida Gwaii provided the opportunity for an unplanned natural experiment to investigate 1) the existence of costs in the production of chemical defences by long-lived plants; 2) the effect of defence levels on the choice made by the herbivore; and 3) the effect of this choice in the selection of plants with higher defences. We addressed these questions using the interaction between western redcedar *Thuja plicata* Donn ex D. Don, one of the dominant conifers in these forests, and Sitka black-tailed deer. Western redcedar is a preferred food source of Sitka black-tailed deer (Pojar et al. 1980; Coates et al. 1985).

2. Methods and results

2.1 Are there defences, and is there a cost?

Black-tailed deer were absent from the forests of Haida Gwaii from the last glaciation (10 000 years BP) until their introduction over a century ago (Golumbia et al. this volume). If the production of defences has a cost, western redcedars with high defences should have been at a disadvantage on Haida Gwaii when deer were absent. Hence, existing Haida Gwaii western redcedar should have, on average, lower defences than mainland trees. To test this hypothesis, we selected two plant categories: nursery-grown seedlings and branches from mature trees collected high enough to be out of the reach of deer. As these samples were never exposed to recent deer browsing both on Haida Gwaii and on the mainland, our analysis avoided the confounding effects of induced defences. Trees that provided seeds or branches had already reached adult size when deer were introduced to Haida Gwaii (see details in Vourc'h et al. 2001) and hence were the product of populations and individuals that had never been exposed to deer. We addressed two specific questions: 1) Do deer, on average, prefer Haida Gwaii redcedars that had not evolved with deer or mainland redcedars that did evolve with deer? and 2) Are Haida Gwaii redcedars characterized by reduced chemical defence compared with those from the mainland?

To test whether deer preferred Haida Gwaii or mainland redcedars, we conducted food choice experiments using seedlings and branches. To investigate the differences in chemical defences, we analyzed leaf terpene content in these samples, terpenes being abundant in redcedar leaves (Vourc'h et al. 2001). Terpenes are known to potentially play a role in chemical defence against herbivores (Lewinsohn et al. 1991b) and to decrease food consumption by deer (Elliott and Loudon 1987; Danell et al. 1990; Duncan et al. 1994). The seedlings we used were produced by nurseries and were made available through forestry companies. The branches of old western redcedars were collected on the same day on Haida Gwaii and on the nearby mainland. The cafeteria feeding choice experiments were performed at three sites on Haida Gwaii. At each of these sites, free-ranging black-tailed deer were offered a choice between Haida Gwaii and mainland individual redcedars. For both types of samples (old trees and seedlings), more plants from Haida Gwaii were browsed than plants from the mainland (Fig. 1). The analyses of the chemical composition showed that Haida Gwaii leaves had on average less monoterpenes than mainland ones, but that was not the case for diterpenes. Total diterpenes were in much smaller quantities than monoterpenes (see details in Vourc'h et al. 2001).

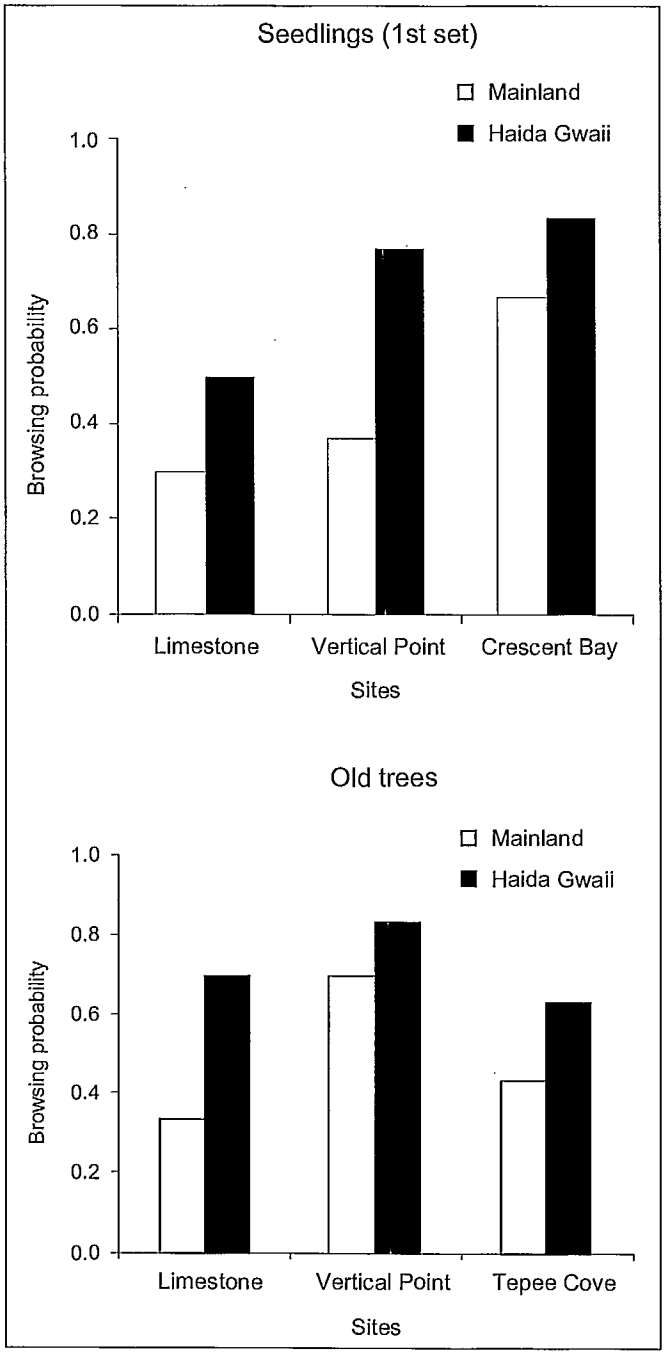
On the basis of these results, we decided to experimentally test the effect of monoterpenes on deer choice (see details in Vourc'h et al. 2002a). When deer were offered the choice between standardized food without or with monoterpenes at concentrations found in western redcedar leaves, deer made an unambiguous choice for monoterpene-free food (see Fig. 2).

These results suggest that, on average, Haida Gwaii redcedars that have not been exposed to browsing by deer for thousands of years are less defended. If it is assumed that the original redcedars that colonized Haida Gwaii after the last glaciation originated from mainland stock that had been subject to browsing, the lower concentrations of terpenes in current stock support the hypothesis that the production of defences is costly to the tree and diminishes in the absence of constant selection.

2.2 Which trees can escape deer?

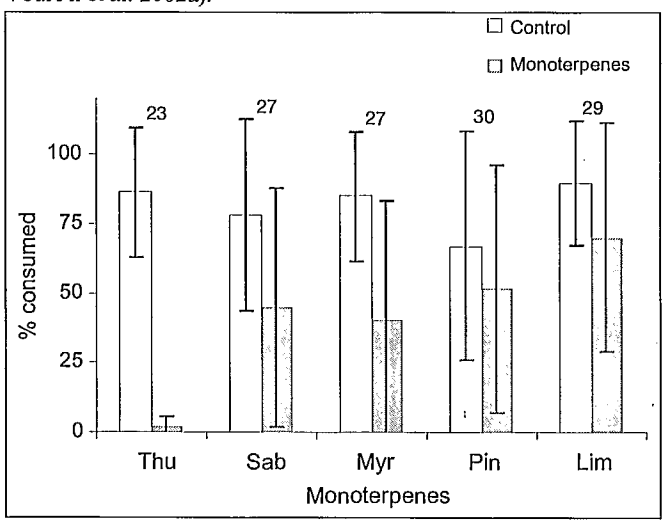
The introduction of Sitka black-tailed deer to Haida Gwaii and the resulting current high deer densities in the forests of Haida Gwaii have provided a unique situation to further investigate the mechanisms involved in the interaction between Sitka black-tailed deer and western redcedar, a situation simplified by the absence of any other large herbivore in the study sites and the paucity of insect herbivores feeding on western redcedars (Fowells 1965; Furniss and Carolin 1977). Martin and Daufresne (1999) showed that western redcedar recruitment is virtually eliminated by deer browsing in old-growth forests, and Martin and Baltzinger (2002) showed that redcedar is severely reduced in second-growth forests following clearcutting. Martin and Baltzinger (2002) also produced evidence that the actual amount of cedar regeneration in these young forests was directly under the control of deer. They sampled sites differing in their accessibility to hunters, on the assumption that where there was more hunting, there would be less browsing pressure from deer. Their results showed that cedar regeneration was significantly

Figure 1
Probability of browsing of redcedar seedlings (first set of the two sets that were tested) and branches of old trees in food choice experiments with Sitka black-tailed deer on three sites in relation to the geographic origin of samples (from Vourc'h et al. 2001).



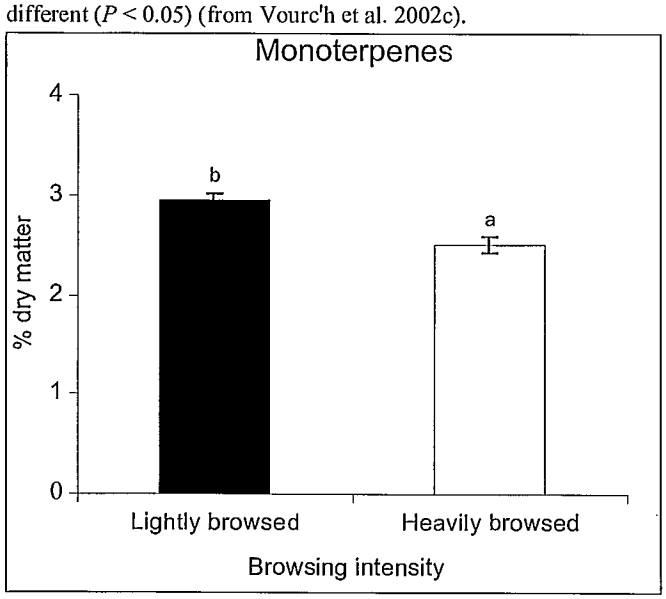
better in sites easily accessible to hunters and that indices of browsing stress on redcedar, as well as on other selected plant species, was lower at these sites. Another point of interest in these regenerating forests was the occurrence side by side of heavily browsed, stunted young redcedars and young redcedars with a normal shape and few signs of browsing. To understand this variation in browsing impact, we sampled heavily and lightly browsed young trees on each of three clearcut sites. Chemical analysis showed that heavily browsed redcedars had a lower total concentration

Figure 2
Average percentage of apples consumed by Sitka black-tailed deer in trials with different monoterpene solutions at *in vivo* redcedar concentration or with a control solution. Number of trials per deer varied from 3 to 5 (with some exceptions). Numbers above bars are number of trials. Vertical bars are standard deviations. Thu = α,β-thujone, Sab = sabinene, Myr = myrcene, Pin = α-pinene, and Lim = *d*+*l*-limonene. All differences in consumption between control and monoterpene bowls are significant ($P < 0.05$) (from Vourc'h et al. 2002a).



of monoterpene than lightly browsed ones (Fig. 3). There was no correlation between browsing intensity and nutrient content: heavily browsed redcedars were actually of lower nutritive value (less nitrogen and more lignin) (Vourc'h et al. 2002c). Because heavily and lightly browsed trees were collected on the same sites and usually side by side, all trees were equally accessible to deer. For similar reasons, we could exclude any effects of the local environment on defence levels.

Figure 3
Means with standard error bars of total monoterpene concentrations in heavily and lightly browsed young western redcedars on the three clearcut sites on Haida Gwaii. Different letters mean that means are different ($P < 0.05$) (from Vourc'h et al. 2002c).



Three other explanations are possible for the observed difference in terpene browsing impact: the age of the tree, its browsing history, and its genetic aptitude to produce defences.

2.2.1 Age and browsing history

Vourc'h et al. (2001) showed that monoterpene concentrations were low in 1-year-old seedlings and reached a peak at the sapling stage. If lightly browsed trees are simply older, escaping deer browsing becomes only a matter of time, happening when the tree is able to produce enough defences. However, we determined the age of the trees by dendrochronology and showed that, at least in two of the three sites, heavily and lightly browsed trees were of the same age (Fig. 4). Ring width series used to determine age also provided information on the trees' history of environmental stress (see Cook and Kairiukstis 1990). By decreasing the annual growth of branches (and consequently leaf formation and photosynthetic rate), deer browsing has a strong effect on overall growth and hampers radial growth until the young trees manage to grow above the browsing limit (Vila et al. 2001, 2002, 2003). Narrow rings in young trees therefore indicate high browsing stress, broad rings absence of or low browsing stress. What we found is that both heavily browsed and lightly browsed redcedars experienced the same low growth pattern until the growth rate of currently lightly browsed trees diverged and increased (see example at Graham, Fig. 5). This suggests that all trees experienced similar browsing pressures until some trees started to escape deer. These results, in addition, rule out the hypothesis that individual differences in browsing history could explain the observed co-occurrence of lightly and heavily browsed trees. All trees had been browsed initially.

Finally, several works have shown that the defoliation of evergreens can, in some cases, trigger induced defences (Marpeau et al. 1989; Lewinsohn et al. 1991a; Lerdau et al. 1994; Litvak and Monson 1998) or, if severe enough, decrease defences (Bryant et al. 1983; Tuomi et al. 1991; Raffa and Smalley 1995). We therefore examined the potential for induced defences in western redcedar to assess if it could explain some of the variation in browsing stress and in shape that we observed for young trees on Haida Gwaii. This was done experimentally with the help of artificial defoliation. Defoliation did not produce any significant change in monoterpene concentrations (see details in Vourc'h et al. 2003), suggesting tentatively that the variations we observed between individuals were constitutive and were reflecting genetic differences in the ability to produce defences independently of browsing. However, as recent results have shown that induced defences can be triggered by chemicals in the saliva from the herbivore rather than by the trauma (e.g., Agrawal et al. 1999; Franceschi et al. 2002), this result should be interpreted prudently.

2.2.2 Genetic variation

A direct way to test for genetic variation in monoterpene production would be to take seeds from heavily and lightly browsed young trees, plant them in a common garden experiment, and look at their monoterpene concentration under natural growing conditions. To allow for natural growing conditions, we would have to wait for at least 5 years before sampling their leaves for chemical analyses. Instead, we used a two-pronged indirect approach. First, we monitored changes in defence concentration of 10- to 15-year-old heavily or lightly browsed young trees that we individually protected from deer. If their levels of defence are genetically controlled, their respective terpene concentrations should remain unchanged after protection and

Figure 4
Mean age of lightly and heavily browsed young western redcedars at the three sites (NG = North Graham, SG = South Graham, NM = North Moresby). Vertical bars are standard errors. ** = statistically different means ($P < 0.01$) (from Vourc'h et al. 2002c).

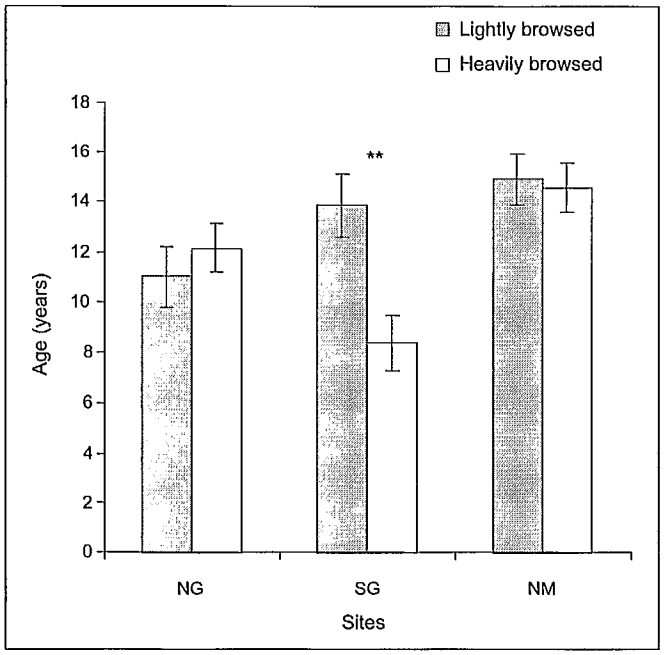
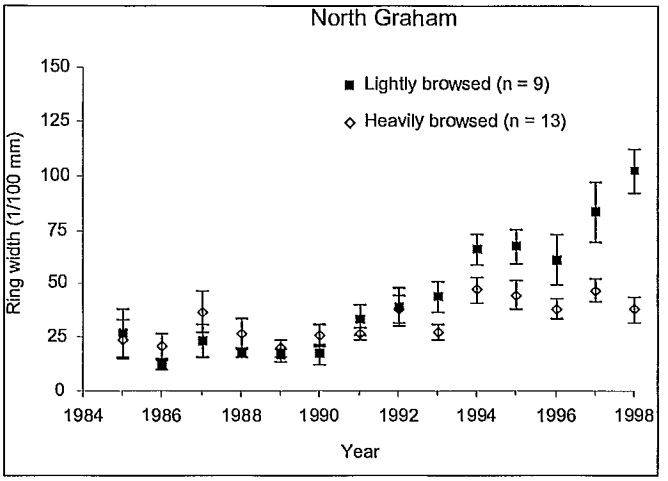


Figure 5
Mean ring widths of lightly and heavily browsed young western redcedars at North Graham, by year. Vertical bars are standard errors. Means are shown when at least three trees per category per site are present for a given year. The numbers (n) in parentheses are the total number of trees (from Vourc'h et al. 2002c).



remain similar to those observed for unprotected trees. This experiment was started in spring 2000. So far, no changes in monoterpene concentrations have occurred (Fig. 6). Second, we took advantage of a genecology study of western redcedar in which 2500 trees originating from 62 open-pollinated families representing 14 populations from British Columbia were planted in 1996 at Holt Creek, Vancouver Island. The seedlings were protected from deer browsing for the first 4 years using plastic cones. After this, the protections were removed and browsing stress was monitored. We found that the total monoterpene concentration was, on average, higher in families where fewer individuals were browsed. This further supports the idea that monoterpene concentrations are genetically controlled in western redcedar (Fig. 7) (see details in Vourc'h et al. 2002b).

Finally, these results were anecdotally confirmed through the observation that out of 15 10-year-old western redcedars that had been planted as ornamentals in Tlell, Haida Gwaii, 14 were heavily browsed, while one was left untouched. The comparison of their chemistry showed that the unbrowsed tree had a much higher monoterpene concentration than the other 14 trees (Fig. 8).

In summary, our results suggest that under strong browsing pressure, very young trees were equally browsed, and only those trees having the genetic potential to eventually produce effective defences ultimately escaped. In the course of development, young trees that are well defended can progressively produce more foliage and thus allocate more resources to growth and defence. Young trees that do not have the genetic potential to produce sufficient monoterpenes cannot deter deer browsing and become caught in a vicious circle of heavy browsing and consequent poor growth (Machida 1979; Bryant et al. 1983; Tuomi et al. 1991; Raffa and Smalley 1995). This suggests that deer can be responsible for the selection of the most defended redcedars in the population. However, one should bear in mind that this process can take place only where redcedar regeneration is possible and abundant enough.

Figure 6
Means with standard error bars of total monoterpene concentrations in heavily and lightly browsed young western redcedars. Half of them were protected from deer browsing by wire cage in April 2000. * = statistically different means between heavily and lightly browsed young trees (protected and unprotected together), $P < 0.05$; ** = $P < 0.01$ (from Vourc'h 2001).

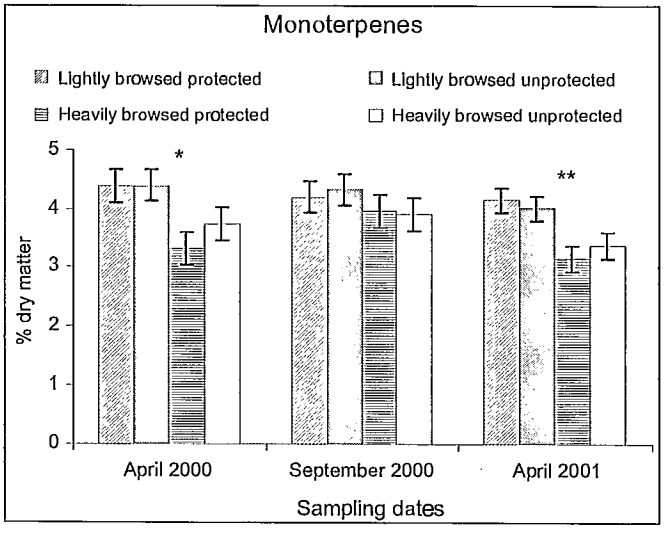


Figure 7
Mean total monoterpene concentrations in individuals from four open-pollinated families for western redcedar grown at Holt Creek, Vancouver Island. Ten, eight, eight, and nine genets were sampled in families 16-3, 5-6, 4-2, and 22-1, respectively. Family number reads as follows: 16-3; 16 = population number, 3 = open-pollinated family number. Vertical bars are standard error. *** = $P < 0.001$ (from Vourc'h et al. 2002b).

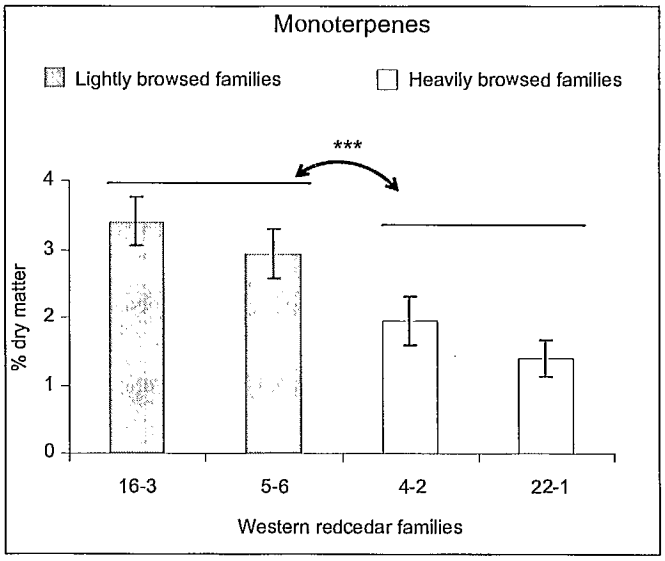
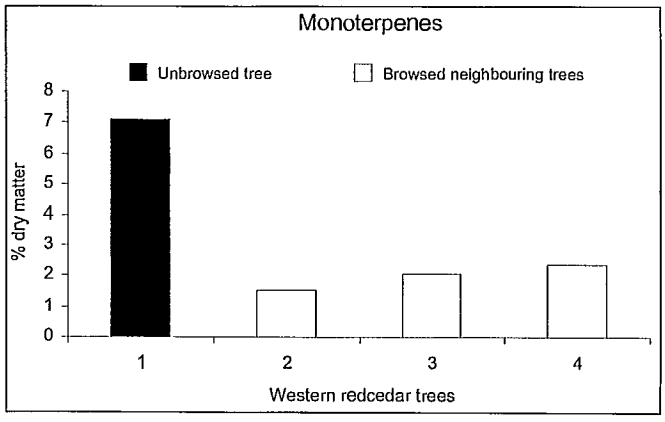


Figure 8
Total monoterpene concentrations in browsed and unbrowsed western redcedars grown at Tlell, Haida Gwaii (from Vourc'h et al. 2002b).



2.2.3 How do lightly browsed redcedars in Haida Gwaii compare with mainland trees?

We compared the palatability and chemical defences of young trees on Haida Gwaii that showed only light browsing with young western redcedar saplings from the mainland. Branches from nonstunted young western redcedar collected the same day on Haida Gwaii and on the mainland were presented to wild Sitka black-tailed deer on Haida Gwaii as cafeteria feeding experiments. We

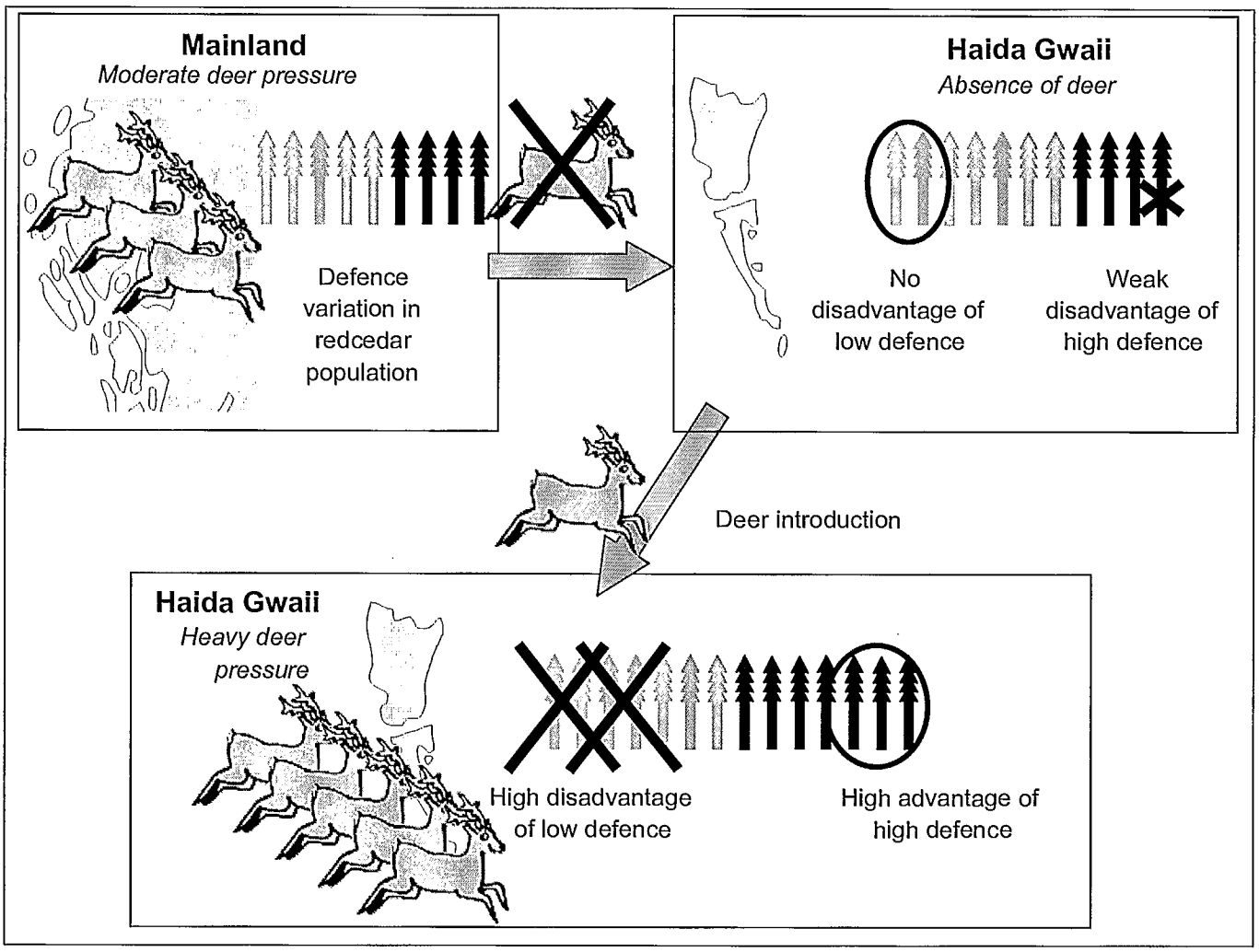
also analyzed their chemical composition. Deer showed no preference between these two samples of trees, and there was no significant difference in their chemical composition (see Vourc'h et al. 2001).

3. Conclusions

Taking as a reference the level of defence typical of redcedar populations under the amount of herbivory they experience on the mainland, our results suggest that in the absence of deer, the proportion of trees with low levels of chemical defences increased in the western redcedar population of Haida Gwaii (hence the higher rate of browsing of the island seedling and old tree samples in the cafeteria experiments) until deer were introduced and started to eliminate the least defended trees (Fig. 9).

The persistence on Haida Gwaii of trees with a potential for defence comparable to that of trees found on the mainland (the results of the cafeteria experiments and chemical analyses on nonstunted saplings) suggests either that the cost of producing these defences was too low to be strongly and/or rapidly counterselected in the absence of deer or that other functions of terpenes, such as protection from photodamage (e.g., Close and McArthur 2002), were maintaining individuals with higher terpene concentrations in the population. When deer were introduced to Haida Gwaii herbivory, pressure increased dramatically to levels higher than on the mainland (Pojar this volume, on the history of vegetation on Haida Gwaii). Under such heavy browsing pressure, trees with low defences were strongly counterselected, in sharp contrast to the hypothesized weak selection against high defences in the absence of deer. It has to be emphasized, however, that this shift towards selection of trees with higher defences can occur only in clearcut sites where regeneration occurs because of a large number of seedlings and an abundance of alternative forage. In old-growth forests, the current rarity of seedlings and of forage in general and the high abundance of deer (see figures in Martin and Baltzinger 2002) result in the elimination of all young redcedar, irrespective of their chemical makeup. In conclusion, these results suggest that deer not only reduce the abundance of western redcedar on Haida Gwaii, but also, under the current browsing pressure, alter the genetic composition of the population. If the variation currently found in the mature trees of Haida Gwaii is to be maintained, we have to find ways to reduce browsing pressure.

Figure 9
Proposed scenario for the evolution of plant defence on Haida Gwaii. The vertical arrows represent western redcedars.



Acknowledgements

We thank Gillian Austin, Isabel Buttler, Craig Ferguson, Janet Gray, Noël Guillon, Laurie Husband, Rob Kelly, Tarmo Põldmaa, Dimitri Rosolowski, Barb Rowsell, and Bevin Wigmore for their help in the field and with various experiments; Tom Clausen, Dominique Gillon, Carol Ritland, and John Russell for insights and help with chemical or genetic analyses; Olympic Forest Products, Husby Forest Products, and Western Forest Products for providing logistic support in the field camps; and last, but not least, John Bryant, Patrick Duncan, Michel de Garine-Wichatitsky, Hervé Fritz, and Yan Linhart for more than helpful insights.

Literature cited

Agrawal, A.A.; Karban, R. 1999. Why induced defenses may be favored over constitutive strategies in plants. Pages 45–61 *in* R. Tollrian and C.D. Harvell (eds.), The ecology and evolution of inducible defenses. Princeton University Press, Princeton, New Jersey.

Agrawal, A.A.; Strauss, S.Y.; Stout, M.J. 1999. Costs of induced responses and tolerance to herbivory in male and female fitness components of wild radish. Evolution 53: 1093–1110.

Barbosa, P.; Schultz, J.C. 1987. Insect outbreaks. Academic Press, New York.

Berenbaum, M.R.; Zangerl, A.R.; Nitao, J.K. 1986. Constraints on chemical coevolution: Wild parsnips and the parsnip webworm. Evolution 40: 1215–1228.

Bryant, J.P.; Julkunen-Tiitto, R. 1995. Ontogenetic development of chemical defense by seedling resin birch: energy cost of defense production. J. Chem. Ecol. 21: 883–896.

Bryant, J.P.; Chapin, F.S.; Klein, D.R. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos 40: 357–368.

Bryant, J.P.; Reichardt, P.B.; Clausen, T.P. 1992. Chemically mediated interactions between woody plants and browsing mammals. J. Range Manage. 45: 18–24.

Chapin, F.S., III; Bryant, J.P.; Fox, J.F. 1985. Lack of induced chemical defense in juvenile Alaska woody plants in response to simulated browsing. Oecologia 67: 457–459.

Close, D.C.; McArthur, C. 2002. Rethinking the role of many plant phenolics—protection from photodamage not herbivores? Oikos 99: 166–172.

Coates, K.D.; Pollack, J.C.; Barker, J.E. 1985. The effect of deer browsing on the early growth of three conifer species in the Queen Charlotte Islands. Research Report 85002-PR, B.C. Ministry of Forests, Victoria, B.C. 13 pp.

Coley, P.D. 1986. Costs and benefits of defense by tannins in a neotropical tree. Oecologia 70: 238–241.

Cook, E.R.; Kairiukstis, L.A. 1990. Methods of dendrochronology. Applications in the environmental sciences. Kluwer Academic Press, Dordrecht, Netherlands.

Danell, K.; Huss-Danell, K.; Bergström, R. 1985. Interactions between browsing moose and two species of birch in Sweden. Ecology 66: 1867–1878.

Danell, K.; Gref, R.; Yazdani, R. 1990. Effects on mono- and diterpenes in Scots pine needles on moose browsing. Scand. J. For. Res. 5: 535–539.

Dirzo, R.; Harper, J.L. 1982. Experimental studies on slug–plant interactions. IV. The performance of cyanogenic and acyanogenic morphs of *Trifolium repens* in the field. J. Ecol. 70: 119–138.

Duncan, A.J.; Hartley, S.E.; Iason, G.R. 1994. The effect of monoterpene concentrations in Sitka spruce (*Picea sitchensis*) on the browsing behaviour of red deer (*Cervus elaphus*). Can. J. Zool. 72: 1715–1720.

Elle, E.; van Dam, N.M.; Hare, J.D. 1999. Cost of glandular trichomes, a "resistance" character in *Datura wrightii* (Solonaceae). Evolution 53: 22–35.

Elliott, S.; Loudon, A. 1987. Effects of monoterpene odors on food selection by red deer calves (*Cervus elaphus*). J. Chem. Ecol. 13: 1343–1349.

Fowells, H.A. 1965. Silvics of forest trees of the United States. Agriculture Handbook No. 271, Division of Timber Management Research, Forest Service, U.S. Department of Agriculture, Washington, D.C.

Franceschi, V.R.; Krekling, T.; Christiansen, E. 2002. Application of methyl jasmonate on *Picea abies* (Pinaceae) stems induces defense-related responses in phloem and xylem. Am. J. Bot. 89: 578–586.

Fritz, R.S.; Hochwender, C.G.; Lewkiewicz, D.A.; Bothwell, S.; Orians, C.M. 2001. Seedling herbivory by slugs in a willow hybrid system: developmental changes in damage, chemical defense, and plant performance. Oecologia 129: 87–97.

Furniss, R.L.; Carolin, V.M. 1977. Western forest insects. Miscellaneous Publication No. 1339, Forest Service, U.S. Department of Agriculture, Washington, D.C.

Hanley, T. 1997. A nutritional view of understanding and complexity in the problem of diet selection by deer (Cervidae). Oikos 79: 209–218.

Karban, R.; Baldwin, I.T. 1997. Induced responses to herbivory. University of Chicago Press, Chicago, Illinois.

Lerdau, M.; Litvak, M.; Moson, R. 1994. Plant chemical defense: monoterpenes and the growth-differentiation balance hypothesis. Trends Ecol. Evol. 9: 58–61.

Lewinsohn, E.; Gijzen, M.; Croteau, R. 1991a. Defense mechanisms of conifers. Differences in constitutive and wound-induced monoterpene biosynthesis among species. Plant Physiol. 96: 44–49.

Lewinsohn, E.; Gijzen, M.; Savage, T.J.; Croteau, R. 1991b. Defense mechanisms of conifers. Relationship of monoterpene cyclase activity to anatomical specialization and oleoresin monoterpene content. Plant Physiol. 96: 38–43.

Litvak, M.E.; Monson, R.K. 1998. Patterns of induced and constitutive monoterpene production in conifer needles in relation to insect herbivory. Oecologia 114: 531–540.

Machida, S. 1979. Differential use of willow species by moose in Alaska. University of Alaska, Fairbanks, Alaska.

Marpeau, A.; Walter, J.; Launey, J.; Charon, J.; Baradat, P. 1989. Effects of wounds on the terpene content of twigs of maritime pine (*Pinus pinaster* Ait.): 2. Changes in the volatile terpene hydrocarbon composition. Trees 3: 220–226.

Marquis, R.J. 1992. Selective impact of herbivores. Pages 301–325 *in* R.S. Fritz and E.L. Simms (eds.), Plant resistance to herbivores and pathogens: ecology, evolution and genetics. University of Chicago Press, Chicago, Illinois.

Martin, J.-L.; Baltzinger, C. 2002. Interaction among deer browsing, hunting, and tree regeneration. Can. J. For. Res. 32: 1254–1264.

Martin, J.-L.; Daufresne, T. 1999. Introduced species and their impacts on the forest ecosystem of Haida Gwaii. Pages 69–85 *in* G.G. Wiggins (ed.), Proceedings of the cedar symposium: growing western redcedar and yellow-cypress on the Queen Charlotte Islands/Haida Gwaii. B.C. Ministry of Forests/ Canada–British Columbia South Moresby Forest Replacement Account, Victoria, B.C.

Mauricio, R.; Rausher, M.D. 1997. Experimental manipulation of putative selective agents provides evidence for the role of natural enemies in the evolution of plant defense. Evolution 51: 1435–1444.

Palo, R.T.; Robbins, C.T. 1991. Plant defenses against mammalian herbivory. CRC Press, Ann Arbor, Michigan.

Paré, P.W.; Tumlinson, J.H. 1999. Plant volatiles as a defense against insect herbivores. Plant Physiol. 121: 325–331.

Peñuelas, J.; Llusià, J. 2002. Linking photorespiration, monoterpenes and thermotolerance in *Quercus ilex*. New Phytol. 155: 227–237.

Phillips, M.A.; Croteau, R.B. 1999. Resin-based defenses in conifers. Trends Plant Sci. 4: 184–190.

Pojar, J.; Lewis, T.; Roemer, H.; Wilford, D.J. 1980. Relationships between introduced black-tailed deer and the plant life of the Queen Charlotte Islands, British Columbia. Unpublished report, B.C. Ministry of Forests, Smithers, B.C. 63 pp.

Pollard, J.A. 1992. The importance of deterrence: response of grazing animals to plant variation. Pages 216–239 *in* R.S. Fritz and E.L. Simms (eds.), Plant resistance to herbivores and pathogens: ecology, evolution and genetics. University of Chicago Press, Chicago, Illinois.

Raffa, K.F.; Smalley, E.B. 1995. Interactions of pre-attack and induced monoterpene concentration in host conifer defense against bark beetle–fungal complexes. Oecologia 102: 285–295.

Rhoades, D.F.; Cates, R.G. 1976. Toward a general theory of plant antiherbivore chemistry. Recent Adv. Phytochem. 19: 168–213.

Robbins, C.T.; Spalinger, D.E.; Van Hoven, W. 1995. Adaptation of ruminants to browse and grass diets: are anatomical-based browser-grazer interpretations valid? Oecologia 103: 208–213.

Sharkey, T.D.; Yeh, S.S. 2001. Isoprene emission from plants. Annu. Rev. Plant Physiol. Plant Mol. Biol. 52: 407–436.

Simms, E.L. 1990. Examining selection on the multivariate phenotype: plant resistance to herbivores. Evolution 44: 1177–1188.

Simms, E.L. 1992. Costs of plant resistance to herbivory. Pages 392–425 *in* R.S. Fritz and E.L. Simms (eds.), Plant resistance to herbivores and pathogens: ecology, evolution and genetics. University of Chicago Press, Chicago, Illinois.

Snyder, M.A.; Linhart, Y.B. 1998. Subspecific selectivity by a mammalian herbivore: geographic differentiation of interactions between two taxa of *Sciurus aberti* and *Pinus ponderosa*. Evol. Ecol. 12: 755–765.

Swihart, R.K.; Bryant, J.P. 2001. Importance of biogeography and ontogeny of woody plants in winter herbivory by mammals. J. Mammal. 82: 1–21.

Tallamy, D.W.; Raupp, M.J. (eds.). 1991. Phytochemical induction by herbivores. J. Wiley & Sons, New York.

Tuomi, J.; Niemelä, P.; Fagerström, T. 1991. Carbon allocation, phenotypic plasticity, and inducible defenses. Pages 85–104 *in* D.W. Tallamy and M.J. Raupp (eds.), Phytochemical induction by herbivores. J. Wiley & Sons, New York.

Vila, B.; Keller, T.; Guibal, F. 2001. Influence of browsing cessation on *Picea sitchensis* radial growth. Ann. For. Sci. 58: 853–859.

Vila, B.; Vourc'h, G.; Gillon, D.; Martin, J.-L.; Guibal, F. 2002. Is escaping deer browse just a matter of time in *Picea sitchensis*? A chemical and dendrochronological approach. Trees – Struct. Funct. 16: 488–496.

Vila, B.; Guibal, F.; Torre, F.; Martin, J.-L. 2003. Growth change of young *Picea sitchensis* in response to deer browsing. For. Ecol. Manage. 180: 413–424.

Vourc'h, G. 2001. Interactions entre plantes longévives et grands mammifères: Défenses chimiques du thuya géant et herbivorie par le cerf à-queue-noire en Colombie-Britannique (Canada). Ph.D. thesis, Université de Montpellier II, Montpellier, France. 66 pp. + annexes.

Vourc'h, G.; Martin, J.-L.; Duncan, P.; Escarré, J.; Clausen, T.P. 2001. Defensive adaptations of *Thuja plicata* to ungulate browsing: a comparative study between mainland and island populations. Oecologia 126: 84–93.

Vourc'h, G.; de Garine-Wichatitsky, M.; Labbé, A.; Rosolowski, D.; Martin, J.-L.; Fritz, H. 2002a. Monoterpene effect on feeding choice by deer. J. Chem. Ecol. 28: 2411–2427.

Vourc'h, G.; Russell, J.; Martin, J.-L. 2002b. Linking deer browsing and terpene production among genetic identities in *Chamaecyparis nootkatensis* and *Thuja plicata* (Cupressaceae). J. Hered. 93: 370–376.

Vourc'h, G.; Vila, B.; Gillon, D.; Escarré, J.; Guibal, F.; Fritz, H.; Clausen, T.P.; Martin, J.-L. 2002c. Disentangling the causes of damage variation by deer browsing on long-lived tree saplings: A chemical and dendrochronological approach. Oikos 98: 271–283.

Vourc'h, G.; Russell, J.; Gillon, D.; Martin, J.-L. 2003. Short-term effect of defoliation on terpene content in *Thuja plicata*. Ecoscience 10: 161–167.

Wallin, K.F.; Raffa, K.F. 2001. Effects of folivory on subcortical plant defenses: Can defense theories predict interguild processes? Ecology 82: 1387–1400.

Herbivory and the missing understory on Haida Gwaii

Christian Engelstoft, Matthew D. Kirchhoff, and Donald Eastman

Abstract

Since the introduction of deer to Haida Gwaii (Queen Charlotte Islands, British Columbia), understory biomass and deer densities have not been monitored. This study estimated the current understory biomass and relative deer density in old-growth stands below 450 m in elevation. Regressions were used to estimate aboveground biomass (shrubs and herbs), available biomass (potential food for deer), and the amount of biomass eaten by deer. We encountered 13 herb, 6 fern, and 8 shrub species in the 110 sites. The aboveground biomass (excluding salal *Gaultheria shallon*) ranged between 0 and 2137 kg/ha, with an overall mean of 258 kg/ha and a median of 82 kg/ha. The average available biomass was 7 kg/ha with a median of 3 kg/ha, and the mean eaten biomass was 5 kg/ha with a median of 3 kg/ha. Pellet group (PG) counts were used to determine relative deer density. The estimated average density was 402 PG/ha (range 0–1840 PG/ha), and the median was 300 PG/ha. There was no correlation between relative deer density and aboveground or available biomass or between canopy opening and under story biomass. We attributed this lack of correlation to the heavy browsing pressure that had occurred prior to this study. The low occurrence of western redcedar *Thuja plicata* in the understory may result in changes to the future canopy species composition. The low amounts of available biomass in the old-growth stands may cause Sitka black-tailed deer *Odocoileus hemionus sitkensis* to starve during unusually cold winters, but in normal winters the forest mosaic of different seral stages must provide food and cover sufficient for their survival. The results provide baseline data for future restoration and monitoring efforts.

1. Introduction

The objective of this study was to evaluate the effects of Sitka black-tailed deer *Odocoileus hemionus sitkensis* on understory vegetation in remaining tracts of old-growth forests on the main islands of Haida Gwaii (Queen Charlotte Islands, British Columbia). We chose old-growth forests because they were the original forests on Haida Gwaii, and knowledge about them can help provide information for the future preservation of native flora and fauna. Old-growth forests are also important for the survival of deer during unusually severe winters because the canopy intercepts snow, resulting in higher food availability (Kirchhoff and Schoen 1987), and provides thermal cover (Bunnell 1990). If deer forage optimally in the old-growth forests during the winter, one expects that they select areas with the highest amounts of available food. We tested the hypothesis that the aboveground and available shrub biomasses in old-growth forest patches were positively correlated with relative deer density, which potentially could identify a deer density threshold below which desired vegetative conditions could be maintained.

2. Study area

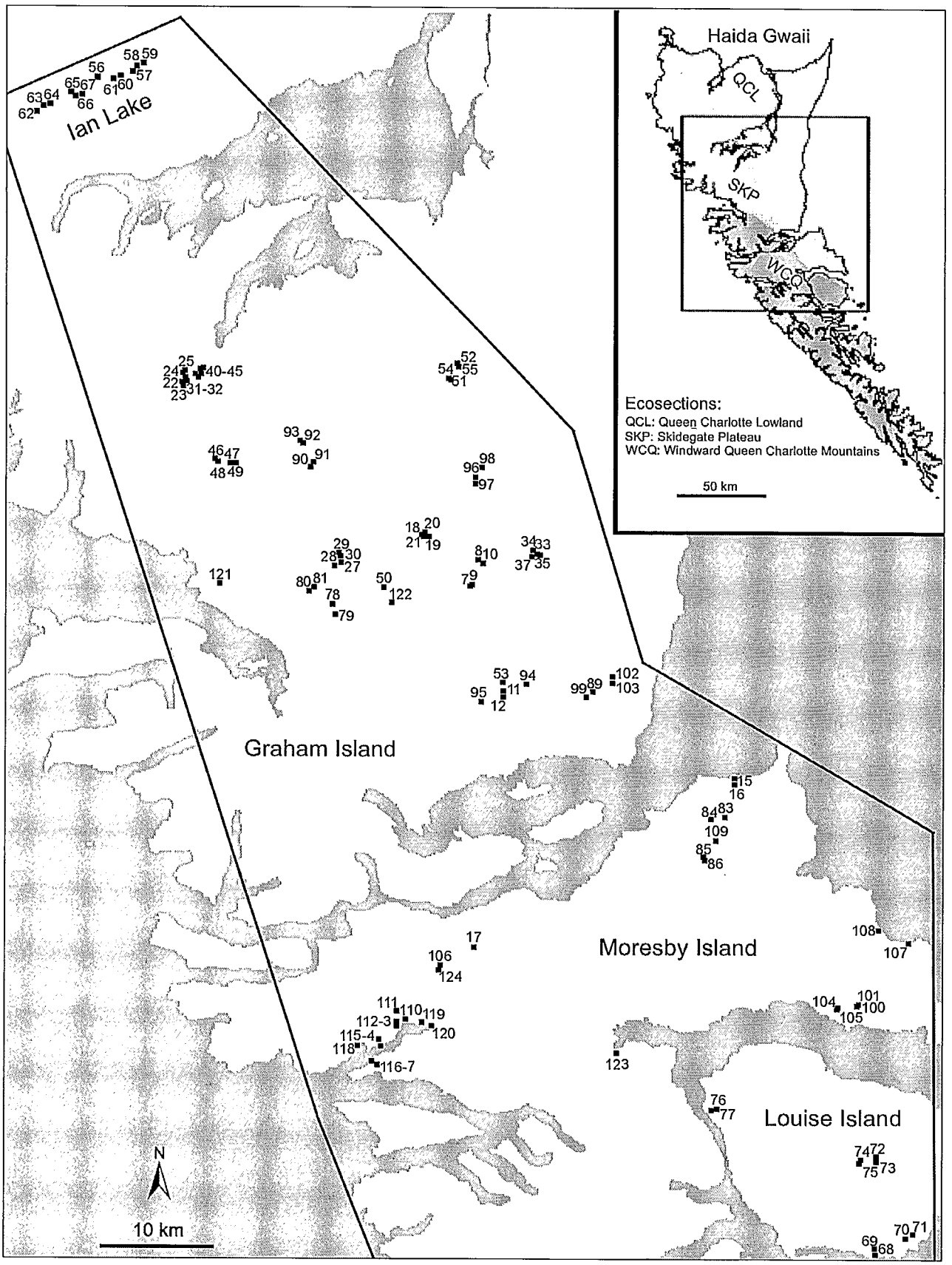
The study took place mainly on the Skidegate Plateau Ecosection (Fig. 1) in the centre of Graham, Moresby, and Louise islands, which consists of land below 500 m above sea level, with forests dominated by western hemlock *Tsuga heterophylla*, Sitka spruce *Picea sitchensis*, western redcedar *Thuja plicata*, and, at higher elevation, yellow-cedar *Chamaecyparis nootkatensis*.

Some sites were also surveyed in the Windward Queen Charlotte Mountains Ecosection and Queen Charlotte Lowland Ecosection (Fig. 1). The Windward Queen Charlotte Mountains Ecosection is mountainous and reaches a maximum elevation of 1148 m. This forest is dominated by western hemlock and western redcedar at lower elevations and mountain hemlock *Tsuga mertensiana* and yellow-cedar at higher elevations. The Queen Charlotte Lowland Ecosection is found in the northeastern part of Haida Gwaii and is an area of low relief, slow drainage, and extensive muskegs and wetlands. The main tree species here are shore pine *Pinus contorta*, western redcedar, and western hemlock (see Pojar et al. 1987 for details).

3. Methods

Most sites were selected to be in old-growth stands that were as ecologically comparable as possible—that is, in similar site series within three biogeoclimatic subzones (Pojar et al. 1987). Since there were insufficient unlogged stands in these site series to meet our desired sample size, we also selected sites in related ecosystems, ensuring that we sampled across a wide range of slopes and aspects below 450 m in elevation.

Figure 1
Study area, sampling locations, and ecosections on Haida Gwaii



3.1 Pellet groups

At each site we sampled pellet group density and vegetation in 1-ha (100 × 100 m) study plots. For pellet group densities, we established three 100 × 1.66 m transects, spaced 25 m apart, with the centre transect bisecting the plot (Engelstoft 2001). Along each transect line, we counted all pellet groups centred within the transect that contained more than 10 pellets (Resource Inventory Committee 1998).

3.2 Vegetation biomass

We chose the nondestructive regression approach, which has been widely used to estimate the biomass of ungulate browse and other woody plants (Telfer 1969; Alaback 1986; Schwab and Pitt 1987; Dyck and Shay 1999). Aboveground and available biomasses were estimated for each sampling area by adding the results from species-specific regression functions that were developed for the study area.

We used power functions to estimate the amount of aboveground biomass because they had good fits (Table 1) and because they always yielded positive values for all diameter measurements. We compared estimates from our power equations with traditional log–log transformation procedures and found that the estimates were similar (ANOVA, $F_{3,9352} = 0.7273$, $P = 0.5355$).

Along the pellet group transects, we established 4-m² shrub plots at 20-m intervals and 1-m² herb plots at 10-m intervals. In the herbaceous plots, we listed all herbs present, counted stems of deer fern *Blechnum spicant* and bunchberry *Cornus canadensis*, and estimated herbivory as a percentage of bunchberry and deer fern.

To estimate bunchberry biomass (g/m²), we used a model developed by Alaback (1986). This model used percent ground cover, so we converted the bunchberry stem count into percent ground cover by assuming that each individual plant covered 0.008 m². The percent cover estimates were divided into the two ranges used in the model (see Alaback 1986 for details).

A model was developed for estimating deer fern biomass. Several authors have developed models to estimate deer fern biomass using parameters such as frond length (Alaback 1986), length and width of frond (Smith and McLeod 1992), and percent cover (Yarie and Mead 1989). The fit (r^2) of these models varied between 0.78 and 0.97. Because deer often eat the tip of the frond, the length of frond was not a feasible measurement. We developed a regression using the stem diameter below the first set of leaves as an independent variable to estimate biomass of deer fern (Table 1).

We estimated aboveground biomass and available biomass in the shrub plots. To estimate aboveground biomass, we used basal stem diameter as an independent variable (Table 1). We identified all plant species and counted all rooted stems. We sampled a subset of basal stem diameters and used regression equations to estimate aboveground biomass (Engelstoft 2001).

To estimate available biomass, we estimated the prebrowsed biomass and subtracted the amount that deer had eaten during previous winters (for details, see Engelstoft 2001). Prebrowsed biomass was estimated by counting the number of twigs of each understory species with diameters <2.4 mm (Engelstoft 2001) and measuring diameters of a subsample of average-size twigs. To estimate the amount of removed biomass we counted the number of points-of-browse (1 year and older) and subsampled the diameters of these (for details, see Engelstoft 2001). To estimate salmonberry *Rubus spectabilis* biomass, we used an equation developed by Alaback (1986), omitting three stem measurements that fell outside the lower range (2–25 mm) of his equation.

Table 1
Functions for estimating aboveground, available, and eaten biomass for selected forage species in old-growth forests on Haida Gwaii

Species	r^2 adj.	Equation[a,b]	Diameter range (mm)	n[c]	No. of sites
Aboveground biomass					
Deer fern *Blechnum spicant*[d]	0.90	$0.0972D^{2.9122}$	0.28–2.63	133	9
Vaccinium spp.[e]	0.94	$0.0739D^{2.6308}$	1.10–20.50	87	15
False azalea *Menziesia ferruginea*	0.98	$0.0309D^{2.902}$	0.86–30.96	27	9
Western redcedar *Thuja plicata*	0.90	$0.1438D^{2.3215}$	1.48–15.11	11	3
Prebrowsed biomass					
Vaccinium spp.[d]	0.66	$0.0759d^{2.5963}$	0.45–3.14	257	15
Eaten biomass					
Vaccinium spp.[d]	0.64	$0.0691x^{2.3871}$	0.38–3.07	323	15
False azalea *Menziesia ferruginea*	0.94	$0.0304x^{3.1563}$	0.71–2.61	7	29

[a] All functions were significant ($P < 0.001$).
[b] D = basal stem diameter (mm), d = basal twig diameter (mm), x = point-of-browse (mm).
[c] n indicates the sample size.
[d] Aboveground and available biomass models are the same.
[e] *Vaccinium* spp. = red huckleberry *V. parvifolium*, oval-leaved blueberry *V. ovalifolium*, and Alaska blueberry *V. alaskaense*.

4. Results

We sampled 110 sites in March and April 2000—72 on Graham Island, 28 on Moresby Island, and 10 on Louise Island (Fig. 1, Table 2)—in 11 different biogeographic site series.

4.1 Total aboveground biomass

Plant species diversity in the understory of old-growth forests was low. We encountered only 13 herb species, 6 fern species, and 8 shrub species (Table 3). The most commonly encountered plants were red huckleberry *Vaccinium parvifolium* (98% of sites), deer fern (95% of sites), and fern-leaved goldthread *Coptis asplenifolia* (45% of sites). Half of the species had frequencies of occurrence of <5%.

Understory biomass varied dramatically. For example, the amount of aboveground biomass for all species, excluding salal, ranged from 0 to 2137 kg/ha, with an overall mean of 258 kg/ha (SD = 388) and a median of 82 kg/ha (Table 4). Of the 110 sites, only 25% of the plots had biomass greater than 363 kg/ha.

Table 2
Frequency of biogeoclimatic site series surveyed on Haida Gwaii according to Skidegate Plateau (SKP), Windward Queen Charlotte Mountains (WCQ), and Queen Charlotte Lowland (QCL) ecoregions and Graham, Louise, and Moresby islands (site series were based on terrestrial ecosystem maps)

Islands/ biogeoclimatic site series[a]	Ecoregions					
	SKP		WCQ		QCL	
	Graham	Moresby	Moresby	Louise	Graham	Total
CWHvh1 HS	0	1	7	0	0	8
CWHvh1 RF	0	0	1	0	0	1
CWHvh1 ?	0	0	2	0	0	2
CWHvh2 RF	0	0	1	0	0	1
CWHwh1 SM	26	3	0	3	1	33
CWHwh1 HS	5	0	0	0	2	7
CWHwh1 RF	10	0	0	0	0	10
CWHwh1 RS	0	0	0	2	0	2
CWHwh1 SC	2	1	0	0	0	3
CWHwh1 YG	1	0	0	2	2	5
CWHwh1 ?	14	8	3	0	0	25
CWHwh2 HS	2	0	0	1	0	3
CWHwh2 SM	5	1	0	2	0	8
CWHwh2 ?	2	0	0	0	0	2
Total	67	14	14	10	5	110
Unknown site series	16	8	5	0	0	

[a] The biogeoclimatic site series divides the landscape up in zones (e.g., CWH), subzones (e.g., vh or wh), variants (e.g., 1 or 2), and site series (e.g., HS, RS, SC, SM, RF, or YG).

4.2 Available aboveground biomass

The average available biomass was 7 kg/ha ($n = 91$, SD = 14 kg/ha), generally an order of magnitude smaller than aboveground biomass (Table 4). Available biomass amounts ranged from 0 to 93 kg/ha (median = 3 kg/ha). This range is skewed upwards by two outliers from the same valley on Moresby Island. The third highest amount of available biomass was only 32 kg/ha. The two outliers differed from other sites by being dominated by deer fern or false azalea *Menziesia ferruginea*, not red huckleberry.

The main contributors to available biomass were red huckleberry (42%), deer fern (25%), false azalea (15%), bunchberry (4%), western redcedar (4%), and salmonberry *Rubus spectabilis* (4%), even though the latter contributed at only one site (Fig. 2). Less than 0.5% of aboveground biomass in the understory was available as forage, because most was out of reach of Sitka black-tailed deer, as noted by Pojar and Banner (1982; see also Stockton this volume; Vila and Martin this volume).

The average eaten biomass was 5 kg/ha, with a median of 3 kg/ha ($n = 91$) (Table 4). Only 3% of the aboveground biomass and 59% of the available biomass were consumed.

4.3 Relative deer density

We found a mean pellet group (PG) density of 402 PG/ha (SD = 362 PG/ha, median = 300 PG/ha, range = 0–840 PG/ha, $n = 110$ transects). Pellet group densities were very variable over short distances. For example, in a forest stand with 12 transects located within approximately 300 m of each other, pellet group densities varied between 0 and 800 PG/ha.

Pellet group densities were not correlated with sampling site attributes such as elevation, stand timber volume, slope, and aspect (Engelstoft 2001). However, the median density of pellet groups was statistically lower for sites with a north aspect than for sites with a south aspect, the latter usually considered as better winter ranges ($U = 698$, $n_1 = 25$, $n_2 = 79$, $P < 0.05$). Pellet group densities were only weakly correlated with eaten biomass ($r^2 = 0.1$, $P = 0.002$), suggesting that the deer use these sites for reasons other than foraging.

Table 3
Frequency and importance as forage of understory plant species in old-growth forests on Haida Gwaii ($n = 110$)

Scientific name	Common name	Frequency (%)	Important deer browse[b]
Shrubs			
Vaccinium parvifolium[a]	Red huckleberry	98	v
Gaultheria shallon	Salal	35	v
Thuja plicata	Western redcedar (seedling)	34	v
V. ovalifolium/alaskaense[a]	Oval-leaved/Alaskan blueberry	22	v
Rubus pedatus	Five-leaved bramble	21	
Menziesia ferruginea	False azalea	20	v
Rubus spectabilis	Salmonberry	4	v
Thuja plicata	Western redcedar (sapling)	1	v
Ferns			
Blechnum spicant	Deer fern	95	v
Dryopteris expansa	Spiny wood fern	25	v
Polystichum munitum	Sword fern	12	v
Gymnocarpium dryopteris	Oak fern	5	
Polypodium glycyrhiza	Licorice fern	2	
Athyrium filix-femina	Lady fern	1	v
Herbs			
Coptis asplenifolia	Fern-leaved goldthread	45	
Cornus canadensis	Bunchberry	38	v
Listera cordata	Heart-leaved twayblade	38	
Moneses uniflora	Single delight	38	
Tiarella trifoliata	Foamflower	28	
Lysichiton americanum	Skunk cabbage	5	v
Claytonia sibirica	Siberian miner's lettuce	3	
Maianthemum dilatatum	False lily-of-the-valley	3	
Galium spp.	Bedstraw	2	
Listera caurina	Northwestern twayblade	2	
Linnaea borealis	Twinflower	1	
Veratrum viride	Indian hellebore	1	
Stellaria spp.	Chickweed	1	

[a] When combining *Vaccinium parvifolium* and *V. ovalifolium/alaskaense*, they grew in 99% of the sites.
[b] Following Pojar et al. (1980). v = preferred forage.

Table 4
Summary of aboveground and available biomass (kg/ha) estimates in old-growth forest sampling sites on Haida Gwaii, March and April, 2000

		Vaccinium sp.[d]	*Vaccinium parvifolium*	*V. ovalifolium/ alaskaense*	*Menziesia ferruginea*	*Thuja plicata* (sapling)	*Thuja plicata* (seedling)	*Rubus spectabilis*	*Cornus canadensis*	*Blechnum spicant*	Total biomass (all sites)
Aboveground ($n = 110$)	n[a]	109	108	24	22	1	37	1	42	104	110
	Avg[b]	242	227	19	11	–	1	–	0	3	258
	SD[b]	385	396	99	74	–	2	–	1	9	388
	Med[c]	75	59	0	0	0	0	0	0	1	82
	Max[c]	2134	2134	911	663	1	13	30	3	76	2137
Eaten ($n = 91$)	Avg	3	1	–	0	–	–	–	1	1	5
	SD	4	2	–	0	–	–	–	7	1	8
	Med	1	0	–	0	–	–	–	0	0	3
	Max	22	17	–	2	–	–	–	59	10	63
Available ($n = 91$)	Avg	3e	4	–	1	–	1	–	0	2	7
	SD	6	7	–	10	–	2	–	1	8	14
	Med	0	1	–	0	–	0	–	0	1	3
	Max	32	45	–	92	–	13	–	3	76	93

[a] n = the number of sites where the plant grew.
[b] Avg = average in all sites, SD = standard deviation.
[c] Med = median, Max = maximum.
[d] *Vaccinium* sp. is *Vaccinium parvifolium* and *V. ovalifolium/alaskaense* combined.

Figure 2
Plant species composition of available biomass for the understory vegetation in old-growth forests on Haida Gwaii. *Cornus canadensis* = Cc, *Blechnum spicant* = Bs, *Vaccinium* spp. = Vac, *Menziesia ferruginea* = Mf, *Thuja plicata* saplings = Tp, *Thuja plicata* seedlings = sTp, and *Rubus spectabilis* = Rs.

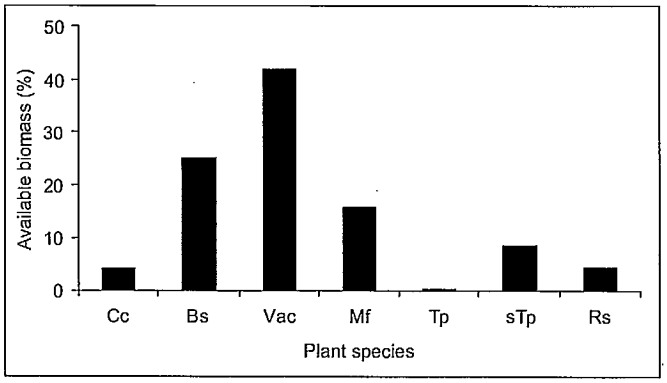
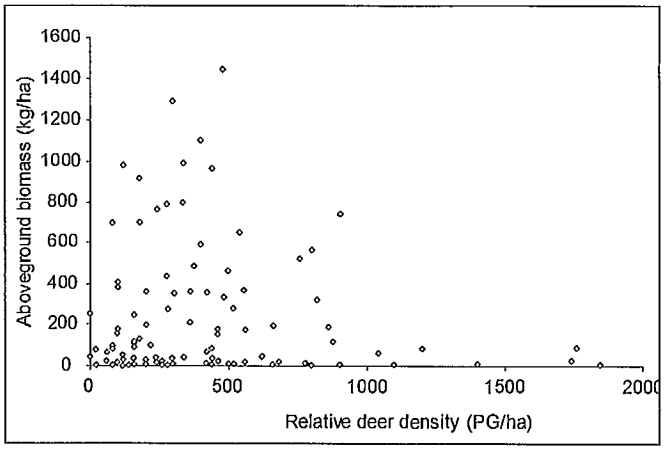
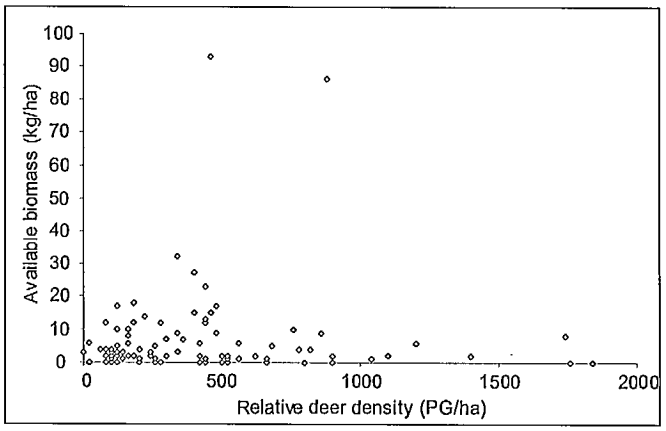


Figure 3
The relationship between estimated aboveground biomass and pellet group densities (PG/ha) in old-growth forests on Haida Gwaii ($n = 91$)



Pellet group densities did not appear to differ among islands, ecosections, and ecological sites. Mean pellet group densities were similar on Graham, Moresby, and Louise islands (Kruskal Wallis $\chi^2 = 0.178$, $P = 0.915$, df = 2), as were densities for the three different ecosections (Kruskal Wallis $\chi^2 = 2.641$, $P = 0.267$, df = 2). At the site series level, no statistical differences in pellet group densities could be detected (Kruskal Wallis $\chi^2 = 4.905$, $P = 0.428$, df = 5). There was no statistical correlation between aboveground and available biomasses and pellet group density, even though it appeared that both measures of vegetation biomass were low where pellet group densities exceeded 950 PG/ha (Figs. 3 and 4).

Figure 4
The relationship between available biomass and pellet group densities in old-growth forests on Haida Gwaii ($n = 91$)



5. Discussion

Relationships between controlling factors and associated response variables are complex in many ecosystems (Garvey et al. 1998). For instance, forest understory varies considerably (Ovington 1962), with biomass affected by canopy closure (Chang et al. 1995), aspect (Klein 1979), and substrate (Peek et al. 1971; Dodd et al. 1972; Alaback 1982; Alaback and Sidle 1986; Messier et al. 1989; Saunders and Puettmann 1999). However, the expected inverse correlation between canopy closure and aspect was not seen on Haida Gwaii. We found no correlation between deer density and either aboveground or available biomass, although eaten biomass was weakly correlated with relative deer density. We suggest that prolonged intensive herbivory by high densities of deer eliminated correlations that typically exist in forested ecosystems where deer have coevolved with vegetation and were controlled through climatic stress or predation.

To our knowledge, there are no understory biomass estimates for old-growth forests on main islands of Haida Gwaii. However, comparisons of understory vegetation diversity and cover in old-growth stands on islands with and without deer (Stockton this volume), coupled with the experimental removal of deer and monitoring of understory vegetation on islands with a long history of browsing (Gaston et al. this volume), have shown that a long history of browsing by deer results in a 90% reduction in the cover of understory vegetation. Some biomass estimates are available from second-growth forest. Three deer exclosures built on Moresby Island showed that protected shrub biomass was 20 times greater than in areas subjected to herbivory (Bennett 1996). These results support our finding that browsing has a major impact on the understory biomass on the main islands as well.

Areas inaccessible to deer, such as old stumps and root wads, are often the only remaining sizable understory "islets." The most abundant plant, red huckleberry, also contributed the most available deer forage. The median amount of the estimated available biomass of red huckleberry on Haida Gwaii was 1 kg/ha. On Vancouver Island and in southeast Alaska, red huckleberry is the most sought-after shrub species, and evidence of browsing is found on most plants.

Although western redcedar was often a prominent member of the forest canopy, we found western redcedar saplings only in one sampling site and found more than one seedling in 41% of the sites. The apparent lack of western redcedar regeneration confirms the findings of Vila and Martin (this volume) in old-growth stands and of Bennett (1996) and Martin and Baltzinger (2002) in regenerating forests after clearcutting. This lack of recruitment of western redcedar may ultimately result in a change of forest canopy composition (see Vila and Martin this volume). Such browsing-induced changes have been observed in other areas of North America (Banner et al. 1983; Stromayer and Warren 1997).

We had expected to find strong relationships between aboveground, available, and eaten biomasses and relative deer density, similar to those demonstrated in Alaska (Kirchhoff 1994). In Alaska, deer density increased significantly with increased biomass of red huckleberry (Kirchhoff 1994). However, we could not detect this relationship in Haida Gwaii. Surprisingly, neither aboveground biomass nor available biomass estimates in these old-growth stands were correlated with relative deer densities (Figs. 3 and 4). This could suggest that the deer use the old-growth stands for reasons other than foraging (e.g., shelter). This might also partly be caused by the temporal difference between the biomass estimates and the relative deer density estimates. For example, pellet group persistence on Haida Gwaii is likely less than a year (6–8 months in southeast Alaska, where weather conditions are similar; Schoen et al. 1985). The biomass estimates, on the other hand, reflect the cumulative history of browsing for more than 6 years (Engelstoft, unpubl. data).

Because deer in general rely on old-growth stands for winter ranges, the low amounts of accessible forage may cause deer to starve during severe winters. However, their survival in normal winters shows that the forest mosaic of different seral stages must provide food and cover sufficient for their persistence. Despite the remaining uncertainties in our understanding of the relations between deer abundance and understory biomass, our estimates of relative deer densities and understory biomass in old-growth stands should provide valuable baseline data for future restoration efforts on Haida Gwaii (Appendix 1).

Acknowledgements

We thank the British Columbia Conservation Foundation for financial support. We thank Weyerhaeuser for logistical support, including the use of a vehicle. We thank Todd Golumbia (Parks Canada Agency), Jean-Louis Martin, and Tony Gaston for comments that improved the manuscript.

Literature cited

Alaback, P.B. 1982. Dynamics of understory biomass in Sitka spruce–western hemlock forests of southeast Alaska. Ecology 63: 1932–1948.

Alaback, P.B. 1986. Biomass regression equations for understory plants in coastal Alaska (USA): Effects of species and sampling design on estimates. Northwest Sci. 60(2): 90–103.

Alaback, P.B.; Sidle, R.C. 1986. Biomass, structure and nutrients of riparian vegetation on a small watershed on Chichagof Island, southeast Alaska. Pages 135–165 *in* D.L. Cornell and M.D. Edgewater (eds.), Watershed perspectives. Smithsonian Environmental Research Center, Washington, D.C.

Banner, A.; Pojar, J.; Trowbridge, R. 1983. Ecosystem classification of the Coastal Western Hemlock Zone, Hypermaritime Subzone (CWHhm), Prince Rupert Forest Region. B.C. Ministry of Forests, Smithers, B.C. 255 pp.

Bennett, J. 1996. The effect of deer browsing on shrub and herbaceous plant growth and cedar regeneration in Sewell Inlet, Queen Charlotte Islands. Report R8-5 F2421-20, Western Forest Products Ltd., Campbell River, B.C. 21 pp.

Bunnell, F.L. 1990. Ecology of black-tailed deer. Pages 31–63 *in* J.B. Nyberg and D.W. Janz (eds.), Deer and elk habitats in coastal forests of southern British Columbia. Special Report Series No. 5, B.C. Ministry of Forests, Victoria, B.C.

Chang, K.T.; Verbyla, D.L.; Yeo, J.J. 1995. Spatial analysis of habitat selection by Sitka black-tailed deer in southeast Alaska, USA. Environ. Manage. 19(4): 579–589.

Dodd, C.J.H.; McLean, A.; Brink, V.C. 1972. Grazing values as related to tree-crown covers. Can. J. For. Res. 2: 185–189.

Dyck, B.S.; Shay, J.M. 1999. Biomass and carbon pool of two bogs in the Experimental Lakes Area, northwestern Ontario. Can. J. Bot. 77(2): 291–304.

Engelstoft, C. 2001. Effects of Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) on understory in old-growth forests on Haida Gwaii (Queen Charlotte Islands), British Columbia. M.Sc. thesis, University of Victoria, Victoria, B.C.

Garvey, J.E.; Marschall, E.A.; Wright, R.A. 1998. From star charts to stoneflies: Detecting relationships in continuous bivariate data. Ecology 79(2): 442–447.

Kirchhoff, M.D. 1994. Effect of habitat fragmentation on deer in southeast Alaska. Federal Aid in Wildlife Restoration Final Research Report, Grant W-23-3,4,5, W-24-1,2, Study 2.10, Alaska Department of Fish and Game, Douglas, Alaska. 60 pp.

Kirchhoff, M.D.; Schoen, J.W. 1987. Forest cover and snow: Implications for deer habitat in southeast Alaska. J. Wildl. Manage. 51(1): 28–33.

Klein, D.R. 1979. Ecology of deer range in Alaska. Pages 25–32 *in* Sitka black-tailed deer: Proceedings of a conference. Report R10-48, Alaska Department of Fish and Game, Juneau, Alaska.

Martin, J.-L.; Baltzinger, C. 2002. Interaction among deer browsing, hunting, and tree regeneration. Can. J. For. Res. 32: 1256–1264.

Messier, C.; Honer, T.W.; Kimmins, J.P. 1989. Photosynthetic photon flux density, red to far-red ratio, and minimum light requirement for survival of *Gaultheria shallon* in western red cedar–western hemlock stands in coastal British Columbia (Canada). Can. J. For. Res. 19(11): 1470–1477.

Ovington, J.D. 1962. Quantitative ecology and the woodland ecosystem concept. Pages 103–192 in J.B. Cragg (ed.), Advances in ecological research. Academic Press, London, U.K.

Peek, J.M.; Krefting, L.W.; Tappeiner, J.C. 1971. Variation in twig diameter–weight relationships in northern Minnesota. J. Wildl. Manage. 35(3): 501–507.

Pojar, J.; Banner, A. 1982. Old-growth forests and introduced black-tailed deer on the Queen Charlotte Islands, British Columbia. Pages 247–257 *in* W.R. Meehan, T.R. Merrell, Jr., and T.A. Hanley (eds.), Fish and wildlife relationships in old-growth forests: Proceedings of a symposium held in Juneau, Alaska, 12–15 April 1982. American Institute of Fishery Research Biologists, Morehead City, North Carolina.

Pojar, J.; Lewis, T.; Roemer, H.; Wildford, D.J. 1980. Relationships between introduced black-tailed deer and the plant life of the Queen Charlotte Islands, British Columbia. Unpublished report, B.C. Ministry of Forests, Smithers, B.C.

Pojar, J.; Klinka, K.; Meidinger, D.V. 1987. Biogeoclimatic ecosystem classification in British Columbia. For. Ecol. Manage. 22: 119–154.

Resource Inventory Committee. 1998. Ground-based inventory methods for selected ungulates: moose, elk and deer. *In* Standards for components of British Columbia's biodiversity. 33 Version 2.0. Victoria, B.C.

Saunders, M.R.; Puettmann, K.J. 1999. Effects of overstory and understory competition and simulated herbivory on growth and survival of white pine seedlings. Can. J. For. Res. 29(5): 536–546.

Schoen, J.W.; Kirchhoff, M.D.; Thomas, M.H. 1985. Seasonal distribution and habitat use by Sitka black-tailed deer in southeastern Alaska. Federal Aid in Wildlife Restoration Final Report, Project W-17-11, W-21-1, W-21-2, W-22-3, W-22-3, and W-22-4, Job 2.6R, Alaska Department of Fish and Game, Juneau, Alaska. 44 pp.

Schwab, F.E.; Pitt, M.D. 1987. Comparison of direct and an indirect method for estimating available winter browse. Wildl. Soc. Bull. 15(4): 544–548.

Smith, N.J.; McLeod, A. 1992. Equations for estimating browse biomass of red huckleberry, western red-cedar, and deer fern by vertical profile. West. J. Appl. For. 7(2): 48–50.

Stromayer, K.A.K.; Warren, R.J. 1997. Are overabundant deer herds in eastern United States creating alternate stable states in forest plant communities? Wildl. Soc. Bull. 25(2): 227–234.

Telfer, E.S. 1969. Twig weight–diameter relationships for browse species. J. Wildl. Manage. 33(4): 917–921.

Yarie, J.; Mead, B.R. 1989. Biomass regression equations for determination of vertical structure of major understory species of southeast Alaska (USA). Northwest Sci. 63(5): 221–231.

Appendix 1
Old-growth stand baseline data of aboveground biomass, available biomass, and relative deer density on Haida Gwaii in late winter 2000

Site no.	UTM zone	Easting	Northing	PG/ha	Aboveground biomass	Available biomass	Salal index
7	8	687220	5918220	240	766		0
8	8	687960	5920400	100	156	2	0
9	8	687350	5918400	300	1298		0
10	8	688300	5920160	400	592	15	0
11	8	689960	5909350	60	2391		0
12	8	689960	5909650	480	1708	17	0
15	9	308281	5901949	0	45		95
16	9	308281	5901299	460	152		51
17	8	687630	5888730	820	326	4	0
18	8	683320	5922420	760	518	10	0
19	8	683450	5922380	900	745	0	0
20	8	683540	5922560	540	648		0
21	8	683380	5922530	160	249		0
22	8	663616	5934816	280	7		0
23	8	663746	5934576	280	272		0
24	8	663896	5935768	700	1991		0
25	8	663720	5935658	380	485		1
27	8	676590	5920157	340	994	32	0
28	8	676180	5919940	480	334	9	0
29	8	676518	5920964	360	210		0
30	8	676612	5920780	480	1446		0
31	8	664160	5935084	360	359	7	0
32	8	664036	5935324	520	279	1	0
33	8	692440	5921080	180	131	2	0
34	8	692340	5921260	60	68	4	0
35	8	692380	5920940	560	372		1
36	9	305200	5941470	120	0		0
37	8	692640	5921040	440	32	13	0
40	8	665268	5936220	60	24		0
41	8	665100	5936072	800	572		0
42	8	664960	5935300	0	255	3	0
43	8	664700	5935600	240	37	2	0
44	8	665360	5935920	80	698	12	0
45	8	665340	5935540	120	47	10	0
46	8	666400	5928620	300	35	2	0
47	8	667658	5928300	660	3	1	0
48	8	666680	5928380	140	2		0
49	8	666920	5928466	160	7		0
50	8	680200	5918160	400	1109	27	18
51	8	685560	5935180	20	76	6	832
52	8	686330	5936320	1200	85	6	119
53	8	689960	5910380	440	977	23	1
54	8	685420	5935380	100	158	4	265
55	8	686230	5936500	200	205	0	527
56	8	658220	5959600	120	15	2	32
57	8	659640	5960420	1100	8	2	0
58	8	659960	5960680	200	366	1	0
59	8	660380	5960480	520	177	0	0
60	8	659120	5959580	120	1	0	0
61	8	658700	5959950	260	14	1	425
62	8	652500	5957490	440	2	1	0
63	8	652680	5957630	900	5	2	0
64	8	652900	5957630	800	1	0	0
65	8	654730	5958630	780	5	4	0
66	8	655080	5958340	440	0	0	0
67	8	655500	5958500	100	13	3	0
68	9	316620	5862040	560	14	1	0
69	9	316600	5862480	520	8	2	0
70	9	319120	5863120	440	4	0	0
71	9	319800	5863440	260	3	0	0
72	9	317340	5870060	680	17	5	715
73	9	317300	5869740	500	4	2	306

Appendix 1 (continued)
Old-growth stand baseline data of aboveground biomass, available biomass, and relative deer density on Haida Gwaii in late winter 2000

Site no.	UTM zone	Easting	Northing	PG/ha	Aboveground biomass	Available biomass	Salal index
74	9	316080	5869910	140	3	1	0
75	9	316080	5869810	300	3	2	0
76	9	304360	5874940	120	12	5	752
77	9	304660	5875060	80	0	0	0
78	8	676000	5916840	280	787	12	6
79	8	676240	5916000	180	695	12	0
80	8	674180	5917860	80	95	2	0
81	8	674520	5918160	260	0	5	0
83	9	307250	5898850	100	178	2	0
84	9	306250	5898600	340	42	3	0
85	9	305200	5895700	620	48	2	0
86	9	305400	5895500	200	28	4	0
89	8	697302	5909680	120	978	17	0
90	8	674140	5928100	160	36	8	0
91	8	674440	5928380	80	93	4	0
92	8	673420	5930040	120	15	2	0
93	8	673360	5930160	160	6	2	2
94	8	691750	5910320	1760	87	0	0
95	8	688250	5908840	860	199	9	0
96	8	687570	5927200	440	85	12	272
97	8	687680	5926910	460	21	15	172
98	8	688200	5928050	220	100	14	469
99	8	696640	5909270	300	362	7	0
100	9	316720	5882480	1740	23	8	137
101	9	316940	5882580	1400	3	2	147
102	8	698850	5910550	180	918	18	0
103	8	698850	5910800	420	358	6	0
104	9	315060	5882300	1040	57	1	0
105	9	315220	5882500	1840	6	0	0
106	8	684900	5887150	880	120	86	0
107	9	321400	5887250	660	202	0	62
108	9	301950	5887500	200	3	0	1
109	9	306420	5896980	160	90	10	0
110	8	682100	5882750	20	3	0	0
111	8	681450	5883350	140	9	3	0
112	8	681450	5882600	160	113	6	3
113	8	681400	5882100	100	410	1	4
114	8	680050	5880650	420	9	0	0
115	8	680000	5881050	100	379	0	0
116	8	679350	5879300	420	70	2	2
117	8	679800	5879050	80	76	2	0
118	8	678250	5880600	280	435	0	0
119	8	683400	5882500	240	15	3	0
120	8	684250	5882200	120	27	3	0
121	8	666780	5918380	560	177	6	64
122	8	680760	5916950	340	798	9	51
123	8	699350	5880050	500	462	0	546
124	8	684750	5886750	460	178	93	0
Average				402	258	7	55
Standard deviation				362	388	14	159
Maximum				1840	2137	93	832
N				110	110	91	110
Median				300	86	3	0

The effects of deer on invertebrate abundance and diversity

Sylvain Allombert and Jean-Louis Martin

Abstract

We compare invertebrate communities among six islands of the Haida Gwaii (Queen Charlotte Islands, British Columbia) archipelago that vary in their history of browsing by introduced Sitka black-tailed deer *Odocoileus hemionus sitkensis*. Invertebrates from the understory vegetation and from the litter were analyzed separately. For the former, there was a strong decrease in both invertebrate abundance and species richness as the length of browsing history increased. For the latter, the abundance and species diversity of invertebrates did not show a uniform response to browsing history across the different categories of invertebrates analyzed. We analyzed this contrast between understory and litter invertebrate communities as resulting from the difference in nature of deer impact on the understory vegetation and on the litter. While the former habitat is progressively reduced and simplified, the latter habitat remains widespread but undergoes qualitative changes as a result of deer impact on the vegetation producing the litter. Overall, deer browsing causes a cascade of effects across the different components of the invertebrate community.

1. Introduction

Species interactions have been recognized as having a major role in shaping communities (Roughgarden and Diamond 1986). Direct interactions between individual species (competition, herbivory, parasitism) have been intensively studied (e.g., see Crawley 1983; Schoener 1983), providing a better understanding of how communities are structured (Cody 1974; Lawton and Strong 1981; Huntly 1991). The importance of indirect effects in structuring communities has been acknowledged more recently (Strauss 1991), as well as the need to focus on a community context to better understand the functioning of ecosystems (Kareiva 1994). The impact of deer on the plant communities of Haida Gwaii (Queen Charlotte Islands, British Columbia) (Stockton this volume) is a dramatic example of the forces at play in plant–herbivore interactions and confirms results from other plant communities (Laws 1970; Hobbs 1996; Waller and Alverson 1997). Interactions between plants and most invertebrates and the dependence of invertebrate abundance and diversity on the structure, abundance, and diversity of the vegetation have also been established (Murdoch et al. 1972; Siemann et al. 1998). However, the unique context of the islands in Laskeek Bay provides a natural experiment (Diamond 1983) to test the importance of indirect effects in shaping communities (e.g., Stockton this volume). We expected that the strong decrease in plant abundance and diversity caused by deer browsing has consequences for the invertebrates associated with the understory, where deer impact concentrates. Furthermore, changes in the understory vegetation should affect litter and soil quality (Pastor et al. 1988; Suominen et al. 1999a; Wardle et al. 2001) and hence impact the litter fauna.

To test these predictions, we compared invertebrate communities in the understory vegetation and the litter on islands varying in browsing history by comparing invertebrate species richness and abundance.

2. Material and methods

We used six of the seven islands (all except South Low) used to compare deer browsing impact on the vegetation (Stockton this volume). Two were deer free, two had deer for less than 20 years, and two had deer for more than 50 years. The same plots used for the vegetation (Stockton this volume) were used to separately sample litter and understory vegetation invertebrates.

2.1 Invertebrate sampling and identification

The invertebrates of the understory vegetation (the vegetation below the browse line 1.5 m above the ground) were sampled on each island in the 5 forest interior plots and in a random subset of 5 of the 10 forest edge plots used by Stockton (this volume) to study deer impact on the vegetation. We swept the vegetation with a 53-cm sweeping net to catch invertebrates, which were removed using a suction aspirator. All the vegetation within a 3.6-m-radius circle centred on the plot centre was swept during 2 minutes (forest edge plots) or during 3 minutes (forest interior plots) at a constant speed. Three samples were collected on each plot at different dates between 25 May and 20 July 2001. Sampling dates for the different islands were interspersed to avoid temporal biases (see Table 1). All arthropods (except Acari) were killed in ethyl acetate fumes and counted. Most were pinned or mounted on points, but excess numbers of

common species or species better preserved in liquids were preserved in 70% ethanol.

Litter invertebrates were sampled in the five forest interior plots only, using pitfall traps consisting of a plastic cup sunk in the ground, its rim levelled with the ground so that crawling invertebrates would fall in. The traps were filled with an equal amount of water and ethylene glycol used as preservative. A few drops of detergent were added to reduce surface tension and facilitate drowning. A ceramic tile, supported on sticks, formed a roof to prevent rain from filling the traps. Six pitfall traps were laid out at each station, spread at equal intervals around a 3-m-diameter circle centred on the plot centre. Traps were left for about 20 days in May–June 2000 (see Table 2). After retrieval, all invertebrates were counted and identified at least to class. Insects, arachnids, and gastropods were then rinsed in water and preserved in 70% ethanol for further identification in the laboratory.

Samples were transferred to the Royal British Columbia Museum for analysis. For understory invertebrates, all specimens were sorted, and molluscs and insects (except Thysanoptera [Thrips] and Nematocera [long-horned flies, a relatively small subset of the Diptera order]) were assigned to morphospecies—i.e., species defined by using morphological character. The use of morphospecies is considered suitable to assess differences in species richness across different habitats (Oliver and Beattie 1996). Other invertebrate groups (mainly spiders) were identified only to order. For litter invertebrates, only molluscs and beetles (Coleoptera) were sorted and identified to morphospecies or species. All identifications to morphospecies were made by the same person (SA). Difficult groups were or are still being verified by specialists and identified to the species (see list in Acknowledgements). Although the present analysis is preliminary, a more in-depth analysis did not alter the overall patterns (Allombert et al. 2005).

2.2 Data analysis

We first estimated differences in abundance between communities by analyzing the number of specimens of a specific group of invertebrates (morphospecies, family, order...) caught in a sample. Second, we estimated differences in species richness by analyzing the number of species of a specific group of invertebrates caught in a plot or on an island.

To determine statistical trends in abundance and diversity in relation to browse, we used simple correlations between the length of browsing history (0, <20, or >50 years) and the variables studied. All probabilities presented were those associated with correlation tests. Only probabilities <0.05 were considered significant. To illustrate the importance of deer in determining inter-island differences (number of specimens, number of species), we defined a deer impact factor: the ratio of the value of each variable on deer-free islands divided by their value on islands colonized for more than 50 years. Deer impact factors are presented only when a significant correlation was found with deer browsing history.

3. Browsing history and understory invertebrates

3.1 Results

Sampling by sweeping yielded exclusively arthropods, all insects apart from a few arachnids. We estimated differences in abundance between communities by looking at the total number of arthropod specimens (minus Acari) caught in each sample. In forest edge plots, we caught a mean of 36.3 specimens per plot on islands without deer and 2.8 on islands with deer for more than 50 years—a 13-fold difference. On islands colonized for less than 20 years,

Table 1
Dates of invertebrate sampling by sweeping net in 2001

Browsing history	Island	Forest edge sampling				Forest interior sampling			
		1st	2nd	3rd	Mean date	1st	2nd	3rd	Mean date
No deer	Low	10 June	30 June	19 July	29 June	4 July	19 July	24 July	15 July
	Lost	2 June	25 June	11 July	22 June	11 July	–[a]	24 July	17 July
<20 years	West Skedans	28 May	11 June	9 July	15 June	15 July	22 July	24 July	20 July
	South Skedans	5 June	18 June	18 July	23 June	15 July	18 July	24 July	19 July
>50 years	Haswell	25 May	23 June	10 July	19 June	10 July	16 July	23 July	16 July
	West Limestone	9 June	26 June	15 July	26 June	15 July	18 July	23 July	18 July

[a] For logistic reasons, forest interior plots were sampled only twice on Lost Island.

Table 2
Dates and duration of invertebrate sampling by pitfall trap in 2000

Browsing history	Island	Set-up date	Sampling date	Mean date	Duration (days)
No deer	Low	22 May	9 June	31 May	18
	Lost	7 June	26 June	16 June	19
<20 years	West Skedans	25 May	12 June	3 June	18
	South Skedans	29 May	19 June	8 June	21
>50 years	Haswell	2 June	22 June	12 June	20
	West Limestone	26 May	15 June	5 June	20

abundance was intermediate (Fig. 1). The trend was similar in the forest interior, where arthropods were six times as abundant on islands without deer as on those where deer had been present for more than 50 years.

We estimated differences in insect species richness (minus Thysanoptera and Nematocera) at two scales: the plot and the island. At the plot scale, the number of species collected in forest edge plots was 10 times lower on islands with deer for more than 50 years than on islands without deer. Again, islands colonized for less than 20 years were intermediate (Fig. 2), and the trend is similar in the forest interior, with a significant fivefold decrease.

At the island scale, there is a significant 5.6-fold reduction in the number of species on islands with deer for more than 50 years, with a mean of 153 species per island on deer-free islands, 82 on islands with deer for less than 20 years, and 33 on islands with deer for over 50 years ($r = -0.95$, $P = 0.003$).

The analysis of insect communities by order revealed that the five orders most often collected (Diptera, Hymenoptera, Homoptera, Coleoptera, and Heteroptera) all showed a significant decrease in species richness on the islands colonized by deer (Table 3). This decrease ranges from twofold for Coleoptera to over ninefold for Heteroptera and Homoptera.

3.2 Discussion

The differences in abundance shown here might not rigorously represent the actual changes, as sampling efficiency may be affected by differences in vegetation density: the denser the vegetation, the lower, probably, the proportion of arthropods captured. However, as vegetation density is lower on islands browsed by deer, the reduction in abundance we observed on deer-affected islands is probably a conservative estimate.

The differences in species richness are large at both plot and island scales. They are also the reverse of what would be expected from MacArthur and Wilson's (1967) island biogeography theory: the two deer-free islands are the smallest and most isolated of the islands studied and yet have more species than the two larger and less isolated islands, the latter having had deer for more than 50 years. On these grounds, too, our estimate of deer impact should be conservative.

The analysis at the order scale revealed that the decrease in species richness was observed in all major taxonomic groups of insects. We can also note that the orders dominated by herbivores, such as the Heteroptera or Homoptera, are more affected than those with a more varied ecology, such as the Coleoptera, suggesting that the invertebrates most dependent on the understory vegetation are also those most impacted by deer browsing.

Figure 1
Abundance of all arthropods minus Acari in relation to the length of browsing history (forest edge: $r = -0.46$, $P < 0.001$; forest interior: $r = -0.64$, $P < 0.001$)

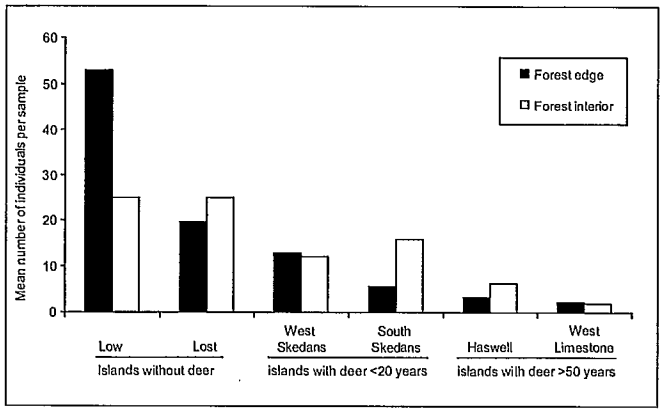


Figure 2
Mean number of invertebrate species per plot in relation to the length of browsing history (forest edge: $r = -0.75$, $P < 0.001$; forest interior: $r = -0.80$, $P < 0.001$)

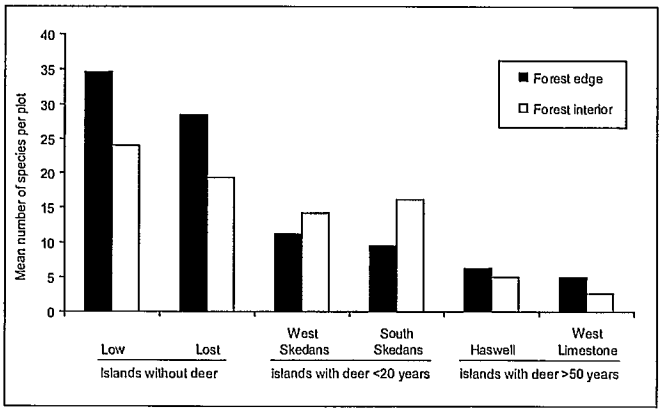


Table 3
Mean number of species in different orders of insects caught per plot by sweeping in relation to browsing history

Browsing history	All orders	Diptera[a] (flies)	Hymenoptera (wasps, bees...)	Homoptera (hoppers...)	Coleoptera (beetles)	Heteroptera (true bugs)	Other orders of insects
No deer	26.55	12.95	8.55	1.85	1.4	1	0.8
<20 years	12.75	7.1	3.35	0.8	0.8	0.05	0.65
>50 years	4.7	2.45	1.3	0.2	0.65	0	0.1
P-value[b]	<0.001	<0.001	<0.001	<0.001	0.035	0.002	0.002
Deer impact factor	5.65	5.29	6.58	9.25	2.15	–	8

[a] The Diptera column is for all Diptera except Nematocera.
[b] Probabilities correspond to the correlation between deer colonization age and the number of species, taking into account all plots.

Finally, we suggest that the higher invertebrate diversity we observed on deer-free islands in forest edge plots compared with interior plots (Fig. 2) results from the higher diversity of plant species observed in forest edge plots (Stockton this volume). This relative difference in invertebrate communities is also observed on islands with a browsing history exceeding 50 years, but the reverse was observed on islands with a browsing history of less than 20 years. This suggests that deer impact on the invertebrate communities is initially faster in forest edge plots but less pronounced in the long term than in interior plots. This is consistent with what was observed for the vegetation: a faster impact of deer on plant cover and species richness in edge habitats (islands with less than 20 years of browsing) but a more severe impact in the interior in the long term (see Stockton this volume).

4. Browsing history and litter invertebrates

4.1 Results

A wide variety of invertebrates were captured in the pitfall traps, with beetles (Coleoptera) predominating. Abundance was estimated for all groups. Species richness was estimated only for snails and slugs (Gastropoda) and beetles (Coleoptera).

Unlike the understory, there was no clear-cut pattern of variation in the number of specimens captured with the history of browsing (Table 4). Millipedes (Diplopoda) were significantly more abundant on islands with at least 50 years of browsing. Snail and slug abundance did not show any significant trend with browsing history ($P = 0.08$); however, their abundance was extremely low on islands with over 50 years of browsing, with more than 8 times fewer specimens caught than on deer-free islands and more than 17 times fewer specimens caught than on islands with a short browsing history. Among ground beetles, those preying on slugs and snails were significantly less abundant on islands colonized by deer, unlike those preying on small arthropods (Table 5).

Species diversity also seemed to vary in its relation to browsing history (Table 6). Ground beetles (Carabidae) and rove beetles (Staphylinidae) showed no variation in species richness, weevils (Curculionidae) and other beetles were more diverse on islands colonized by deer, and snails and slugs (Gastropoda) were less diverse on islands colonized by deer.

4.2 Discussion

The reaction to increasing deer browsing differed markedly between the invertebrate communities of the understory and of the litter. This contrast probably relates to basic differences in the impact of deer on litter and understory vegetation. Understory vegetation is progressively reduced and simplified by deer, whereas the area of litter habitat available to invertebrates is not affected by deer. Rather, it is litter quality that is modified, in numerous and contrasting ways related to local conditions (plant composition, amount of litter, humidity, temperature, aspect, etc.). Hence, a variety of responses is possible, depending on invertebrate biology. One could expect, in theory, an increase in species diversity for some groups. However, the cases of higher species richness that we observed on islands affected by deer have to be interpreted with caution, as those islands were also the largest studied and the closest to the main islands, both features that might be associated with increased species richness (MacArthur and Wilson 1967). So far, other studies have also failed to document systematic changes in litter/soil invertebrates with browsing intensity (Suominen et al. 1999a,b), except for small negative impacts on species richness in some isolated groups (Wardle and Barker 1997; Suominen 1999). The dependence of snails and slugs on fresh or decaying plant tissue nevertheless suggests that the disappearance of deciduous shrubs in the understory of islands colonized for more than 50 years may be a key factor in their lower abundance and diversity on these islands. This lower abundance might in turn be responsible for the lower abundance of gastropod-eating ground beetles on islands colonized by deer, showing that the impact of deer on one group of invertebrates can cascade on their predators.

5. Conclusion

Although the importance of the impact of large herbivores on invertebrates has been investigated in several studies (Wardle and Barker 1997; Rambo and Faeth 1999; Suominen 1999; Suominen et al. 1999a,b), their impact on the invertebrates of the forest understory vegetation had not

Table 4
Mean number of specimens in the different classes of invertebrates caught per interior plot by pitfall traps in relation to deer browsing history

Browsing history	Gastropoda (snails and slugs)	Diplopoda (millipedes)	Arachnida[a] (spiders and daddy-long-legs)	Insecta (insects)	Chilopoda (centipedes)	Malacostraca (litter crustacea)
No deer	0.59	10.04	3.43	119.20	0.80	10.67
<20 years	1.24	10.41	5.72	61.70	0.25	28.93
>50 years	0.07	35.59	6.28	143.29	1.39	22.64
P-value	0.083	<0.001	0.059	0.261	0.076	0.478
Deer impact factor	–	0.28	–	–	–	–

[a] Arachnids correspond to all arachnids but Acari.

Table 5
Mean number of specimens in two groups of ground beetles (Coleoptera: Carabidae) caught per interior plot by pitfall traps in relation to browsing history

Browsing history	Gastropod-eating ground beetles	Other ground beetles
No deer	26.77	78.37
<20 years	13.42	33.97
>50 years	11.29	93.94
P-value	0.015	0.379
Deer impact factor	2.37	–

been studied before. The striking difference we observed in the response of understory and litter invertebrates might reflect, as we suggested, basic differences in impact of deer on the resources used by the invertebrates in the two habitats. In the understory, deer greatly reduce resource quantity (amount of food, laying sites, shelters, etc.) available to invertebrates, especially as the nature of the foliage is drastically different between the understory (mostly broad leaves) and the subcanopy and canopy (mostly coniferous needles), and thus induce an overall invertebrate community impoverishment. For the litter, deer browsing tends to affect the quality of the habitat more than the quantity of habitat available (fewer deciduous leaves, more acidity due to needles, conditions less buffered from wind and sun), leading to specific responses to deer presence by different invertebrate groups.

Our results show that the direct effects of deer on plants (Stockton this volume; Vourc'h et al. this volume; Vila and Martin this volume) cascade into other components of the ecosystem, here the invertebrates, from consumers to predators and parasites. Additional cascading effects might occur, such as the impact that the disappearance of numerous pollinating species may have on pollination or the consequence of changes in the litter and soil fauna for the decomposition process.

Acknowledgements

Special thanks go to people without whom this work would not have been possible: Dave Blades, Isabel Buttler, Rob Cannings, Ian Fuhr, Tony Gaston, Rob Kelly, Greg Martin, Barb Rowsell, Joanna Smith, and Andrew Trant. We also thank Steve Stockton, Todd Golumbia, Marc Creery, Michelle Masselink, Liann Bobechko, Janet Gray, and Joelle Fournier for their help. Numerous taxonomists helped with the identification of insects, including R.S. Anderson (Curculionidae), D. Blades (various groups), D.E. Bright (Scolytidae), R.A. Cannings (Odonata and Asilidae), J.M. Cumming (Empididae), R.W. Duncan (Scolytidae), A. Francoeur (Formicidae), R. Forsyth (Gastropoda), K.G.A. Hamilton (Auchenorrhyncha), G. Pohl (Staphylinidae), and G.G.E. Scudder (Heteroptera).

Literature cited

Allombert, S.; Stockton, S.; Martin, J.L. 2005. A natural experiment on the impact of overabundant deer on forest invertebrates. Conserv. Biol. 19: 1917–1929.

Cody, M.L. 1974. Competition and the structure of bird communities. Princeton University Press, Princeton, New Jersey.

Crawley, M.J. 1983. Herbivory, the dynamics of animal–plant interactions. Blackwell Scientific Publications, Oxford, U.K.

Diamond, J.M. 1983. Laboratory, field and natural experiments. Nature (London) 304: 586–587.

Hobbs, N.T. 1996. Modification of ecosystems by ungulates. J. Wildl. Manage. 60: 695–713.

Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. Annu. Rev. Ecol. Syst. 22: 477–503.

Kareiva, P. 1994. Higher order interactions as a foil to reductionist ecology. Ecology 75: 1–2.

Laws, R.M. 1970. Elephants as agents of habitat and landscape change in East Africa. Oikos 21: 1–15.

Lawton, J.H.; Strong, D.R. 1981. Community pattern and competition in folivorous insects. Am. Nat. 118: 317–338.

MacArthur, R.H.; Wilson, E.O. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.

Murdoch, W.W.; Evans, F.C.; Peterson, C.H. 1972. Diversity and pattern in plants and insects. Ecology 53: 819–829.

Oliver, I.; Beattie, A.J. 1996. Invertebrate morphospecies as surrogates for species: A case study. Conserv. Biol. 10: 99–109.

Pastor, J.; Naiman, R.J.; Dewey, B.; McInnes, P. 1988. Moose, microbes and the boreal forest. BioScience 38: 770–777.

Rambo, J.L.; Faeth, S.H. 1999. Effect of vertebrate grazing on plant and insect community structure. Conserv. Biol. 13: 1047–1054.

Roughgarden, J.; Diamond, J.M. 1986. Overview: the role of species interactions in community ecology. Pages 333–343 *in* J.M. Diamond and T.J. Case (eds.), Community ecology. Harper & Row, New York.

Schoener, T.W. 1983. Field experiments on interspecific competition. Am. Nat. 122: 240–285.

Siemann, E.; Tilman, D.; Haarstad, J.; Ritchie, M. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. Am. Nat. 152: 738–750.

Table 6
Mean number of species of gastropods and three representative groups of beetles caught per interior plot by pitfall traps, in relation to browsing history

		Coleoptera (Beetles)			
Browsing history	Gastropoda	Carabidae	Staphylinidae	Curculionidae	Other families
No deer	1.9	3.7	1.5	1.8	2.2
<20 years	2.1	4	0.7	2.2	1.8
>50 years	0.4	3.5	2.3	3.7	4.1
P-value	0.001	0.544	0.153	<0.001	0.001
Deer impact factor	4.75	–	–	0.48	0.53

Strauss, S.Y. 1991. Indirect effects in community ecology: their definition, study and importance. Trends Ecol. Evol. 6: 206–210.

Suominen, O. 1999. Impact of cervid browsing and grazing on the terrestrial gastropod fauna in the boreal forests of Fennoscandia. Ecography 22: 651–658.

Suominen, O.; Danell, K.; Bergström, R. 1999a. Moose, trees, and ground-living invertebrates: indirect interactions in Swedish pine forests. Oikos 84: 215–226.

Suominen, O.; Danell, K.; Bryant, J.P. 1999b. Indirect effects of mammalian browsers on vegetation and ground-dwelling insects in an Alaskan floodplains. Ecoscience 6: 505–510.

Waller, D.M.; Alverson, W.S. 1997. The white-tailed deer: a keystone herbivore. Wildl. Soc. Bull. 25: 217–226.

Wardle, D.A.; Barker, G.M. 1997. Competition and herbivory in establishing grassland communities: implications for plant biomass, species diversity and soil microbial activity. Oikos 80: 470–480.

Wardle, D.A.; Barker, G.M.; Yeates, G.W.; Bonner, K.I.; Ghani, A. 2001. Introduced browsing mammals in New Zealand natural forests: aboveground and belowground consequences. Ecol. Monogr. 71: 587–614.

The effects of deer and squirrels on forest birds: community structure, population density, and reproduction

Jean-Louis Martin, Sylvain Allombert, and Anthony J. Gaston

Abstract

In this paper, we summarize changes to the forest bird communities of Haida Gwaii (Queen Charlotte Islands, British Columbia) brought about by the introduction of Sitka black-tailed deer *Odocoileus hemionus sitkensis* and red squirrel *Tamiasciurus hudsonicus*. We investigated the relationships between browsing history and both 1) songbird distribution and abundance, using point count censuses and mapping surveys, and 2) songbird reproduction, by analyzing variation in juvenile to adult ratio in birds caught in mist nets, as well as variation in nest predation risk. The results indicate that deer have a greater impact than squirrels on both bird distribution and reproduction. The longer the history of browsing on an island, the lower the abundance of its songbirds, and the lower their reproductive success. As expected, this impact has affected mainly bird species that depend heavily on the understory for foraging or nesting.

1. Introduction

Habitat structural complexity has been viewed as a key factor in explaining the number of bird species living in an area (MacArthur and MacArthur 1961; MacArthur et al. 1962). This relationship is thought to have developed because increased structural diversity provides more niches (higher diversity of foraging sites, food sources, and nest sites). Later studies by Bowman and Harris (1980) and Martin and Roper (1988) developed the idea that increased structural complexity, by providing a variety of different nest sites, decreased the efficiency of nest predators and hence allowed for the coexistence of more bird species than in habitats of simpler structure.

Although the canopy in natural temperate forests can be structurally complex, the understory is where the highest level of structural diversity can be achieved. Most of the species of primary producers coexist in the understory: mosses, fungi, herbaceous plants, shrubs, and regenerating trees. Their abundance depends on climate, soil, and the amount of light coming through the canopy, but also on the nature and abundance of the consumer species and on how these affect plant biomass (see review in Schmitz and Sinclair 1997). Stockton (this volume) showed that, within the islands of Laskeek Bay, the diversity and abundance of the understory vegetation decreased dramatically as the length of time deer had been present increased. Furthermore, Allombert and Martin (this volume) have shown how these changes in understory vegetation have affected the diversity and abundance of associated insects. As vegetation and insects directly and indirectly affect songbird populations (e.g., Sipura 1999), these observations beg the question of how the introduction of deer has affected the forest birds of Haida Gwaii (Queen Charlotte Islands, British Columbia). A high abundance of white-tailed deer *Odocoileus virginianus* has been shown to have a negative impact on songbirds in managed forests of eastern North America (Casey and Hein 1983; DeGraaf et al. 1991; deCalesta 1994). However, the impact of abundant deer on bird communities in natural and protected forests was, until recently, a subject of debate (McShea and Rappole 1997; but see McShea and Rappole 2000). In Europe, also, the need to better understand the consequences of increasing deer population for woodland birds has been increasingly emphasized (Fuller 2001).

In this paper, we revisit the unique situation provided by the islands of Laskeek Bay, to examine the correlation between presence of deer and songbird community structure, population density, and reproduction. Having access to islands with similar browsing history, but with different nest predator assemblages, we attempt to distinguish 1) the relative effects on songbirds of resource depletion by deer and 2) the relative increase in the vulnerability of songbird nests to predators.

Among the nest predators, the introduced red squirrel *Tamiasciurus hudsonicus* is of particular interest. It is known to be a major predator of songbird nests (Ehrlich et al. 1988; Bayne et al. 1997; Darveau et al. 1997; Sieving and Willson 1998) and has become common on some islands (Golumbia et al. this volume). Its impact on songbirds in Haida Gwaii was first documented by Martin and Joron (2003). On the adjacent mainland, Sitka spruce *Picea sitchensis* seeds are the main staple for red squirrel (Banfield 1974; Rusch and Reeder 1978; Gurnell 1983; Sieving and Willson 1998), and this is probably true on Haida Gwaii as well (pers. obs.). The results from this study should improve understanding of how indirect interactions between various community components affect biological diversity in temperate forests (for theoretical reviews on indirect effects in communities, see Strauss 1991; Miller and Travis 1996) and increase our awareness of the costs and/or benefits to native songbirds caused by the introduction of the Sitka

black-tailed deer *Odocoileus hemionus sitkensis* and red squirrel to Haida Gwaii.

2. Deer effect on songbird community structure and population density

We selected for study six of the seven small islands with different histories of deer presence that were used in the study of deer impact on vegetation and insects (Stockton this volume; Allombert and Martin this volume). Two islands (Low and Lost islands) had no history of deer browsing, two islands (South and West Skedans islands) have had deer for less than 20 years, and two (West Limestone and Haswell islands) have had deer for more than 50 years. As in the insect study (Allombert and Martin this volume), the seventh island, South Low (no deer), was not used, because its forested area is too narrow to provide sufficient forest interior conditions for songbirds.

2.1 Methods

Two standard methods were used to collect information on songbird community structure and population density: the point count method (Bibby 1992; Martin et al. 1995) and the spot mapping method (Bibby 1992). We used two of the five standard plots used on each island for the plant and insect work as the centre of two nonoverlapping point count stations, and birds were censused four times in 1999 during the breeding season within 50 m of the centre of each station. The spot mapping was also conducted in 1999 on four morning visits of 4 hours' duration to each island, during which all songbirds and particularly all singing males were mapped. For both methods, all observations were carried out by a single observer (SA).

2.2 Results

Twenty-one species were observed during point counts or spot mapping, 16 of which were breeding on at least one of the islands (Table 1). Two species were considered erratic (Pine Siskin *Carduelis pinus* and Red Crossbill *Loxia curvirostra*). Three were accidentals (Tree Swallow *Tachycineta bicolor*, Red-breasted Nuthatch *Sitta canadensis*, and Wilson's Warbler *Wilsonia pusilla*). The total number of species recorded on the deer-free islands (10 species) was slightly lower than on the islands with deer (14 and 13 species), a result consistent with the smaller area and greater isolation of the deer-free islands (see MacArthur and Wilson 1967; but also see Martin et al. 1995). However, the average number of species observed at a single station during point counts decreased with increasing browsing history (9.5 species on islands with no deer, 7.7 on islands with deer for less than 20 years, 6.0 on islands with deer for more than 50 years) ($F = 19.17$, $P < 0.001$, ANOVA 1). The average number of individual birds recorded in point counts also decreased from about 10 individuals on deer-free islands to 7 on islands with deer for less than 20 years and to 5 or less on islands with deer for more than 50 years ($F = 19.6$, $P < 0.001$, ANOVA 1). The total density of songbirds (total number of pairs per hectare), obtained from the spot mapping method, decreased from 13 pairs/ha on deer-free islands to 11 pairs/ha on islands with deer for less than 20 years and to less than 4 pairs/ha on islands with deer for more than 50 years ($F = 29.6$, $P < 0.05$, ANOVA 1). Finally, when population densities for individual species were examined, the population density of 8 of the 16 breeding species decreased with increasing browsing history (statistically significant for 6, based on point count data; Allombert 1999). Of the eight species that decreased in the presence of deer, six forage and/or breed mainly on the ground or in the ground or shrub vegetation layers. The other two species were the Brown Creeper[1] (feeding and nesting on tree trunks) and the Golden-crowned Kinglet, which makes extensive use of the forest canopy.

2.3 Discussion

Seven species showed highest population densities on islands with the longest history of deer browsing (Table 1). However, most of these species were relatively rare, and the trend was statistically significant for only two of them. The two woodpeckers and the Varied Thrush are the largest species considered and may be more frequent on islands with a long history of deer browsing, simply because these are the largest and least isolated of the islands studied (see MacArthur and Wilson 1967). However, it is notable that three of the species positively correlated to duration of browsing, Hermit and Varied thrushes and Dark-eyed Junco, often feed on the ground in areas of open understory (Godfrey 1986; Jones and Donovan 1996; George 2000). Among thrushes, the two species whose density/abundance increased with increasing browsing history were the least dependent on the understory vegetation. The thrush species most dependent on the understory, the Swainson's Thrush (Morse 1972; Sealey 1974; Godfrey 1986; Evans Mack and Yong 2000), was most abundant on islands with little or no browsing history. Morse (1972), studying the distribution of Hermit and Swainson's thrushes on islands along the coast of Maine, also noted that Swainson's Thrush was more common than Hermit Thrush on small offshore islands, but he tentatively attributed this to competitive exclusion. The four remaining species with higher densities on deer-affected islands were species foraging and/or breeding on trunks (the two woodpeckers already mentioned) or in the canopy (Chestnut-backed Chickadee and Towsend's Warbler). The only species with no identified population abundance trend in either the mapping or the point count data sets was the Pacific-slope Flycatcher, a species hunting flying insects in the subcanopy. There was no significant difference in the number of species recorded per point count or in population densities among islands within island categories (Allombert 1999 and unpubl. data).

To summarize, a long history of deer browsing seems to cause a decrease in the overall abundance of songbirds in the forest. This decrease was mainly caused by a several-fold reduction in a group of common species that are heavily dependent on the vegetation in the ground and shrub layer for feeding and/or nesting. Among the islands used in this study, the red squirrel occurs only on West Limestone Island, one of the two islands with the longest history of

[1] Scientific names of songbird species are given in Table 1.

Table 1
Distribution of songbird species and abundance trend with increasing browsing history obtained from mapping and point count data

Species[a]	Mapping data (number of pairs per hectare)			Point count data (number of individuals per point count)			Trend
	Deer free	Deer present <20 years	Deer present >50 years	Deer free	Deer present <20 years	Deer present >50 years	
Species found in ground, shrub, and subcanopy vegetation layers							
Fox Sparrow *Passerella iliaca*	1.56	2.56	0	1.31	1.06	0	Decreasing
Song Sparrow *Melospiza melodia*	1.85	1.20	0.13	0.63	0.25	0	Decreasing
Hermit Thrush *Catharus guttatus*	0	0.17	0.21		Absent in point counts[b]		Increasing
Varied Thrush *Ixoreus naevius*	0	0.06	0.10		Absent in point counts[b]		Increasing
Swainson's Thrush *Catharus ustulatus*		Late breeder[c]	Absent	0.19	0.31	0	Decreasing
Winter Wren *Troglodytes troglodytes*	1.57	0.98	0.54	1.44	0.69	0.38	Decreasing
Dark-eyed Junco *Junco hyemalis*	0	0.06	0.10		Absent in point counts[b]		Increasing
Rufous Hummingbird *Selasphorus rufus*	1.43	1.38	0	1	1.13	0	Decreasing
Orange-crowned Warbler *Vermivora celata*	2.22	1.75	0.15	2.13	1.56	0.13	Decreasing
Species found mainly in subcanopy and canopy vegetation layers and on tree trunks							
Pacific-slope Flycatcher *Empidonax difficilis*	0.85	0.40	0.49	0.56	0.38	0.50	No trend
Chestnut-backed Chickadee *Parus rufescens*	0	0	0.10	0	0	0.44	Increasing
Golden-crowned Kinglet *Regulus satrapa*	0.94	0.58	0.18	1	0.88	0.69	Decreasing
Townsend's Warbler *Dendroica townsendi*	0.85	0.99	1.31	0.31	0.75	1.88	Increasing
Brown Creeper *Certhia americana*	0.69	0.18	0.15	0.75	0.13	0.19	Decreasing
Hairy Woodpecker *Picoides villosus*	0	0	0.10	0	0	0.06	Increasing
Red-breasted Sapsucker *Sphyrapicus ruber*	0	0.06	0.09	0	0	0.13	Increasing
Number of breeding species	10	14	13				

[a] Species are ranked in relation to habitat preference (from lower to upper layers in the vegetation).
[b] Species present on the islands but not recorded in the point count stations (50 m around the observer).
[c] Migratory species arriving too late on breeding ground to provide sufficient data to assess number of pairs.

deer browsing. There was no significant difference in the songbird community or in population densities between West Limestone Island and the other island with greater than 50 years of deer browsing (Haswell Island), where only native nest predators (mainly crows) occur.

3. Deer and squirrel effects on songbird reproduction

The results above provided only limited indications of how much the reduction in songbird abundance resulted from deer depleting resources for certain songbirds and how much resulted from deer effects causing increased predation on songbird nests. To learn more about the role of the relative importance of these two processes, we chose to compare songbird reproductive success as well as nest predation among islands differing in deer impact and among islands differing in predator assemblage. We used mist nets to catch songbirds just after the start of fledging and estimated reproductive success by the ratio of juveniles to adults on islands that had 1) no introduced species (Low Island), 2) deer for less than 20 years (West Skedans Island), 3) deer for more than 50 years (Reef Island), and 4) deer and squirrels present for more than 50 years (East Limestone Island and Vertical Point on Louise Island). There were no islands with squirrels but without deer. Native predators (corvids) were present on all islands. These comparisons provided estimates of reproductive success that integrated the effects of resources available for reproduction and the effects of nest losses to predators. To better estimate the importance of nest losses, we monitored natural and artificial nests on islands belonging to three of the island categories: islands without introduced species (Low, Lost, and South Low islands), islands with deer for more than 50 years but without squirrels (Reef, Ramsay, and Kunga islands), and islands with deer and squirrels for more than 50 years (East Limestone, Louise, and Lyell islands). Details are given in Martin and Joron (2003).

3.1 Effect of deer and squirrels on postbreeding juvenile to adult ratio

3.1.1 Methods

Mist netting was carried out each summer from 1998 to 2001 on Low Island, Reef Island, and West Limestone Island and at Vertical Point on Louise Island. On West Skedans Island, mist netting was carried out only in 2000 and 2001. All birds captured were identified, aged, and sexed, using the criteria of Pyle (1997). What follows is a summary of preliminary results of this ongoing research.

The total number of birds captured on each island over the study period varied from 507 to 988. Nine species, having a variety of sensitivity to browsing history (see previous section and Table 1), comprised the bulk of adults captured (Table 2).

Because spring weather conditions varied from year to year and influence songbird reproductive success (Gaston et al. 2005), we used the data from Low Island, our

Table 2
Species most commonly captured in mist nets on the different islands[a]

Species	Number of adults caught
Orange-crowned Warbler *Vermivora celata*	201
Townsend's Warbler *Dendroica townsendi*	143
Swainson's Thrush *Catharus ustulatus*	131
Hermit Thrush *Catharus guttatus*	129
Winter Wren *Troglodytes troglodytes*	96
Golden-crowned Kinglet *Regulus satrapa*	87
Fox Sparrow *Passerella iliaca*	85
Pacific-slope Flycatcher *Empidonax difficilis*	59
Song Sparrow *Melospiza melodia*	57

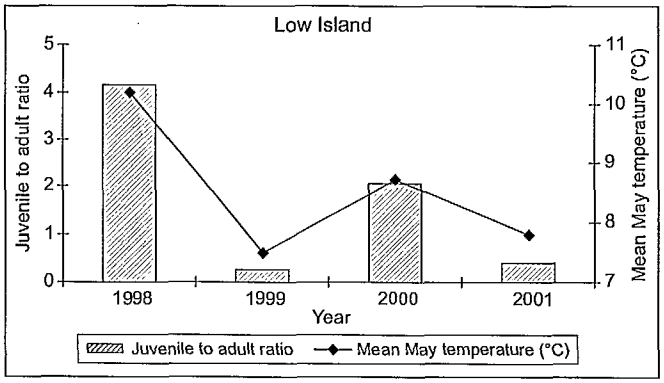
[a] Mist netting occurred on Low Island, Reef Island, and West Limestone Island and at Vertical Point on Louise Island from 1998 to 2001 and on West Skedans Island in 2000 and 2001.

reference island with no introduced species, to get an idea of how weather affected juvenile to adult ratio. On Low Island, the juvenile to adult ratios of the species most often captured (Table 2) were highest during warmer springs and lowest during colder springs (Fig. 1, $R^2 = 0.992$, $P < 0.01$). Because of this, we compared juvenile to adult ratios among island categories separately for colder and warmer springs. We did this by analyzing separately those species, among the nine species listed in Table 2, that were negatively affected by deer (numbers negatively correlated with deer browsing history) and those that were positively affected or unaffected by deer (numbers positively or not correlated with browsing history) (Table 1).

3.1.2 Species negatively affected by deer

During colder springs (1999, 2001), the average juvenile to adult ratio was low and relatively constant on all islands (Fig. 2), although the ratio on the island with deer for more than 50 years but without squirrels was slightly but significantly higher ($P < 0.01$, GLM analysis) than on the other islands. In years with warmer springs, the average juvenile to adult ratio was higher on all islands than in years with colder springs and was highest on the island with no introduced species and lowest for islands with deer for over 50 years (Fig. 2). The decrease in the juvenile to adult ratio with increasing browsing history was highly significant in these species ($P < 0.001$, GLM analysis), and their reproductive success was similar on islands with long browsing history only and on islands with deer and squirrels.

Figure 1
Yearly variation of juvenile to adult ratios on Low Island in relation to weather



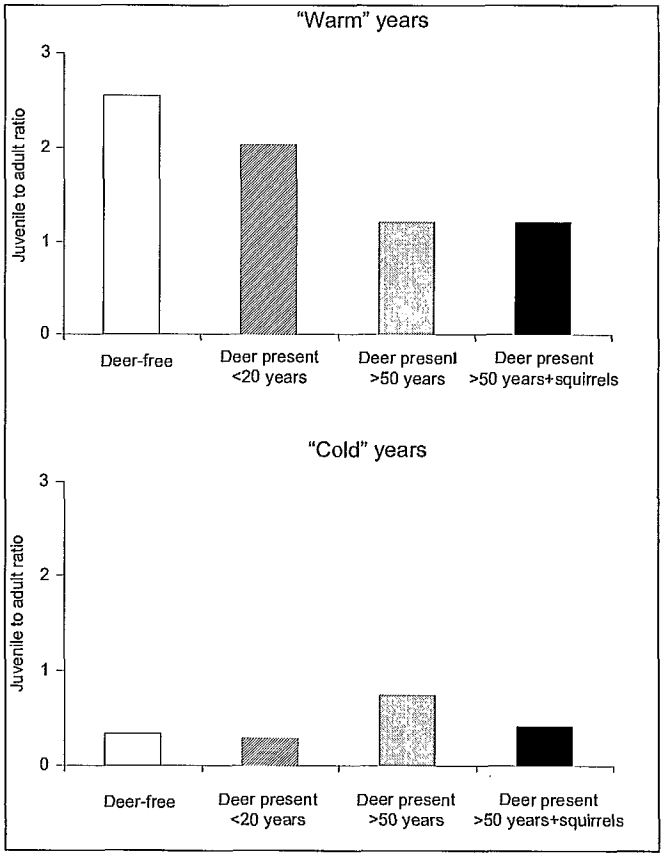
3.1.3 Species positively affected or unaffected by deer

For these species, there was also a marked contrast between lower ratios during colder springs and higher ratios in warmer springs, but their values during warmer springs were less tied to browsing history. The lower sample sizes for this limited number of species preclude any statistical evaluation.

3.1.4 Discussion of juvenile to adult ratios

These results suggest that songbird reproductive potential is higher on islands without introduced deer, enabling them to take greater advantage of good years. On islands with deer for more than 50 years, songbirds have poor reproductive success, whatever the climatic conditions, suggesting that on those islands, deer have become the dominant factor governing songbird reproduction. The higher reproductive success in good years on islands without

Figure 2
Variation in juvenile to adult ratios of deer-sensitive species between island categories during warm springs (top) and cold springs (bottom)



introduced species (but with native avian nest predators) and the lack of a strong effect of squirrel presence on the species most affected by deer browsing suggest resource depletion as the main factor reducing reproductive success in these species.

3.2 Effect of squirrel, native predators, and deer on songbird nesting success

This section summarizes information presented by Martin and Joron (2003).

3.2.1 Methods

We compared losses of natural nests to predators on islands with and without squirrels by searching for nests and revisiting them to determine breeding success. We searched for nests mainly on Reef Island (no squirrels, but deer present for at least 50 years) in forests with mature Sitka spruce and on Louise Island (squirrels and deer for more than 50 years), also in sites with mature Sitka spruce. We also placed artificial nests on nine islands: three with no introduced species (Low, South Low, and Lost islands), three with deer for more than 50 years (Reef, Kunga, and Ramsay islands), and three with squirrels and with deer for more than 50 years (East Limestone, Louise, and Lyell islands). The last three islands varied in the amount of mature Sitka spruce, a key component of squirrel abundance. We used 506 artificial nests placed on the ground or in shrubs along transects on each island to analyze variation of nest predation with predator assemblage and predator habitat. On one island with squirrels (East Limestone), we also used automatic cameras to get direct evidence of which predator was preying upon nests on these islands.

3.2.2 Results

For both natural and artificial nests, the highest predation risk was observed in the presence of squirrels (Tables 3 and 4). All pictures taken with automatic cameras identified red squirrel as the predator, suggesting that on islands with squirrels and crows, squirrels find most nests first. However, predation risk varied among islands with squirrels, being highest in stands with mature conifers, where it fluctuated from year to year in response to fluctuations in squirrel abundance (Fig. 3). These fluctuations were likely caused by fluctuations in Sitka spruce seeds. Vegetation cover around the nest had little effect on nest predation on islands with squirrels.

On islands without squirrels, nest predation increased with decreasing vegetation cover, suggesting that removal of the vegetation by deer increased the risk of predation by native avian nest predators that use visual cues. On these islands, nest predation concentrated near predictable food sources for the main native predators, Northwestern Crows *Corvus caurinus* and Common Ravens *Corvus corax*, such as the intertidal zone where corvids often forage (Godfrey 1986; Martin et al. 1995) or around colonies of seabirds breeding in burrows on the forest floor. Such colonies are intensively visited by crows and ravens looking for eggs, young, or adults to prey upon.

Hence, for open-nesting songbirds, the risk of predation in these forests varies with predator composition, with the openness of the habitat, and with the availability of alternative food (spruce seeds for squirrels, seabirds for crows and ravens).

4. Conclusions

Our results indicate that the introduction of black-tailed deer has had a major impact on the population density of several songbird species, in particular on the species most dependent on the forest understory. This decrease is not compensated for by the higher population densities observed in a few species on islands with the longest history of deer impact. Such an increase on heavily impacted islands can be related to habitat features such as larger, taller trees on the better protected inshore islands or to island geography (larger area and decreased isolation) that increases the likelihood of supporting species such as woodpeckers (see Martin et al. 1995). The analyses of reproductive success and of nest predation suggest that the main effect of deer is through the depletion of resources necessary to songbird reproduction, such as nest sites or insects. This interpretation is consistent with and follows from our results on the impact of deer on understory vegetation (Stockton this volume) and insect communities (Allombert and Martin this volume). The comparison of the results of the juvenile to adult ratio and nest predation studies suggests that although nest predation by squirrels can be important locally, it seems not to be the main factor controlling songbird reproduction. However, Martin and Daufresne (1999), Vila et al. (2002), and Martin and Baltzinger (2002) all suggest that the proportion of spruce in these forests should increase in the future. This could increase the abundance of squirrels and may also increase their impact on songbirds. However, the increase will depend on the age that spruce will be able to reach in the forests of the future.

Table 3
Comparison by CONTRAST (Hines and Sauer 1989) of natural nest survival in absence or presence of red squirrel[a] (from Martin and Joron 2003)

	Without squirrels			With squirrels			Contrast between categories				
	N	s	s^{15}	N	s	s^{15}	Diff. s	χ^2	df	P	SL
Eggs	18	1	1	14	0.922	0.30	0.078	881.7	1	<0.001	***
Nestlings	42	0.990	0.86	22	0.985	0.80	0.005	0.2	1	0.68	n.s.

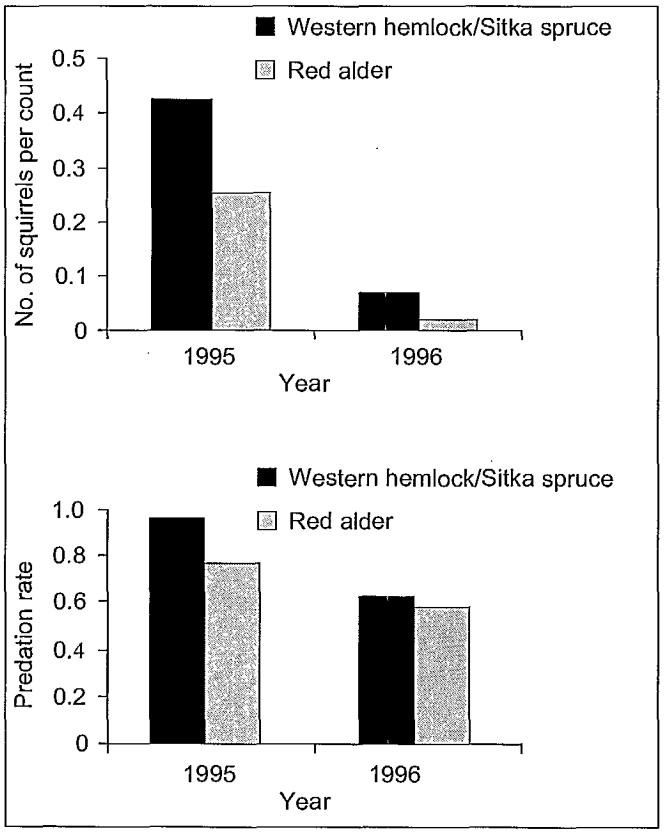
[a] N = number of nests; s = daily nest survival rate; s^{15} = nest survival over a period of 15 days; Diff. s = difference in daily survival rate; χ^2 = chi-squared value of contrast analysis; df = degree of freedom; P = probability value given by contrast analysis; SL = significance level; n.s. = nonsignificant.

Table 4
Comparison by CONTRAST (Hines and Sauer 1989) of nest survival between island categories for artificial nests placed on the ground[a] (after Martin and Joron 2003)

Comparison		Contrast for ground nests				
		Diff. s	χ^2	df	P	SL
I–II	Deer	0.005	1.08	1	0.299	n.s.
II–III	Squirrel	0.013	4.43	1	<0.000 01	***
I–III	Both	0.034	26.84	1	<0.000 01	***

[a] Average nest survival after 15 days (s^{15}) varies from 0.87 on islands with no introduced species (category I) to 0.82 on islands with deer for more than 50 years (category II) and 0.59 on islands with deer and squirrels for more than 50 years (category III). Diff. s = difference in daily survival rate; χ^2 = chi-squared value of contrast analysis; df = degrees of freedom; P = probability value given by contrast analysis; SL = significance level after modified Bonferroni procedure (Simes 1986) was used to correct statistical significance for multiple tests; n.s. = nonsignificant. Results were identical for nests placed in the shrubs.

Figure 3
Relationship between squirrel abundance, habitat type, year, and survival of artificial nests on East Limestone Island.
Top: Variation in the average number of squirrels contacted in a sample of point counts in forest stands dominated by western hemlock *Tsuga heterophylla*/Sitka spruce and in stands dominated by red alder *Alnus rubra* in 1995 and 1996 on East Limestone Island.
Bottom: Variation in survival after 15 days of artificial nests placed on the ground in forest stands dominated by western hemlock/Sitka spruce or by red alder in 1995 and 1996 on East Limestone Island.



Hence, the introduction of a large herbivore in the forests of Haida Gwaii has revealed an intricate web of direct and indirect interactions linking large herbivores, generalist nest predators, and songbirds. It has also provided evidence that the distribution, abundance, and diversity of songbirds might be determined first by higher levels of resources in structurally diverse forests and only second by nest predation. Finally, our results provide an answer to the birders from the mainland who were puzzled by the paucity of songbird activity in the forests of Haida Gwaii (K. Martin and T.E. Martin, pers. commun.). The quietness of spring in the forests of Haida Gwaii is probably, like the open understory, a recent feature on these islands.

Acknowledgements

We thank all those who contributed to the mist-netting effort, especially Sylvie Blangy, Soline Blangy-Martin, Isabel Buttler, Sue Charest, Charlie Cornwallis, Joëlle Fournier, Colin French, Ian Fuhr, Janet Gray, Rob Kelly, Bev McBride, Tarmo Poldmaa, Barb and Keith Rowsell, Joanna Smith, Christophe Tourenq, Andrew Trant, and Georges Yau. Special thanks go to staff and directors of the Laskeek Bay Conservation Society. Finding and monitoring natural and artificial nests were facilitated by Sylvie Blangy, Janet Brown, Isabel Buttler, Lorraine Carson, Ginny Collins, Tanguy Daufresne, Joëlle Fournier, Colin French, Janet Gray, Kathy Heise, Rob Kelly, Sabine Mercier, Marcella Sneiders, and Georges Yau. Sally Aitkin, Doug Burles, Alain Caizergues, Pat Declerc, Bob Elner, Terry and Charlotte Husband, Moira Lemon, Greg Martin, Kathy Martin, Tom Martin, Tarmo Poldmaa, Roger Pradel, Mark Salzl, Katie Sieving, Dan Simberloff, Gwenaël Vourc'h, and Greg Wiggins provided insights or logistic help.

Literature cited

Allombert, S. 1999. Importance des interactions indirectes dans les écosystèmes: un exemple impliquant un cervidé et une communauté d'oiseaux. M.Sc. thesis, University of Montpellier II, Montpellier, France.

Banfield, A.W.F. 1974. The mammals of Canada. National Museums of Canada and University of Toronto Press, Toronto, Ontario.

Bayne, E.M.; Hobson, K.A.; Fargey, P. 1997. Predation of artificial nests in relation to forest type: contrasting the use of quail and plasticine eggs. Ecography 20: 233–239.

Bibby, C.J. 1992. Bird census techniques. Academic Press, London, U.K.

Bowman, G.B.; Harris, L.D. 1980. Effect of habitat heterogeneity on ground nest depredation. J. Wildl. Manage. 44: 806–813.

Casey, D.; Hein, D. 1983. Effects of heavy browsing on a bird community in a deciduous forest. J. Wildl. Manage. 47: 829–836.

Darveau, L.B.; Huot, J.; Mélancon, E.; DeBelleffeuille, S. 1997. Forestry practices and the risk of nest predation in a boreal coniferous forest. Ecol. Appl. 7: 572–580.

deCalesta, D.S. 1994. Effect of white-tailed deer on songbirds within managed forests in Pennsylvania. J. Wildl. Manage. 58: 711–718.

DeGraaf, R.M.; Healy, W.M.; Brooks, R.T. 1991. Effects of thinning and deer browsing on breeding birds in New England oak woodlands. For. Ecol. Manage. 41: 179–191.

Ehrlich, P.R.; Dobkin, D.S.; Wheye, D. 1988. The birder's handbook: a field guide to the natural history of North American birds. Simon and Schuster, New York.

Evans Mack, D.; Yong, W. 2000. Swainson's Thrush (*Catharus ustulatus*). *In* A. Poole and F. Gill (eds.), The Birds of North America, No. 540. The Birds of North America, Inc., Philadelphia, Pennsylvania.

Fuller, R.J. 2001. Responses of woodland birds to increasing numbers of deer: a review of evidence and mechanisms. Forestry 74: 289–298.

Gaston, A.J.; Martin, J.-L.; Allombert, S. 2005. Oceanography affects breeding biology for the terrestrial avifauna of a temperate coastal rainforest. Avian Conservation and Ecology 1:4 [online] URL: http://www.ace-eco.org/vol1/iss1/art4.

George, T.L. 2000. Varied Thrush (*Ixoreus naevius*). *In* A. Poole and F. Gill (eds.), The Birds of North America, No. 541. The Birds of North America, Inc., Philadelphia, Pennsylvania.

Godfrey, W.E. 1986. The birds of Canada. National Museums of Canada and University of Toronto Press, Toronto, Ontario.

Gurnell, J. 1983. Squirrel numbers and the abundance of tree seeds. Mammal Rev. 13: 133–148.

Hines, J.E.; Sauer, J.R. 1989. Program CONTRAST—a general program for the analysis of several survival or recovery rate estimates. Fish and Wildlife Service, U.S. Department of the Interior, Washington, D.C.

Jones, P.W.; Donovan, T.M. 1996. Hermit Thrush (*Catharus guttatus*). *In* A. Poole and F. Gill (eds.), The Birds of North America, No. 261. The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D.C.

MacArthur, R.H.; MacArthur, J.W. 1961. On bird species diversity. Ecology 42: 594–598.

MacArthur, R.H.; Wilson, E.O. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.

MacArthur, R.H.; MacArthur, J.W.; Peer, J. 1962. On bird species diversity. II. Prediction of bird census from habitat measurements. Am. Nat. 96: 167–174.

Martin, J.-L.; Baltzinger, C. 2002. Interaction among deer browsing, hunting, and tree regeneration. Can. J. For. Res. 32: 1254–1264.

Martin, J.-L.; Daufresne, T. 1999. Introduced species and their impacts on the forest ecosystem of Haida Gwaii. Pages 69–85 *in* G.G. Wiggins (ed.), Proceedings of the cedar symposium: growing western redcedar and yellow-cypress on the Queen Charlotte Islands/Haida Gwaii. B.C. Ministry of Forests/ Canada–British Columbia South Moresby Forest Replacement Account, Victoria, B.C.

Martin, J.-L.; Joron, M. 2003. Nest predation in forest birds: influence of predator type and predator's habitat quality. Oikos 102: 641–653.

Martin, J.-L.; Gaston, A.J.; Hitier, S. 1995. The effect of island size and isolation on old growth forest habitat and bird diversity in Gwaii Haanas, Queen Charlotte Islands, Canada. Oikos 72: 115–131.

Martin, T.E.; Roper, J.J. 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. Condor 90: 51–57.

McShea, W.J.; Rappole, J.R. 1997. Herbivores and the ecology of forest understory birds. Pages 298–309 *in* W.J. McShea, H.B. Underwood, and J.H. Rappole (eds.), The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C.

McShea, W.J.; Rappole, J.H. 2000. Managing the abundance and diversity of breeding bird populations through manipulation of deer populations. Conserv. Biol. 14: 1161–1170.

Miller, T.E.; Travis, J. 1996. The evolutionary role of indirect effects in communities. Ecology 77: 1329–1335.

Morse, D.H. 1972. Habitat differences of Swainson's and Hermit thrushes. Wilson Bull. 84: 206–208.

Pyle, P. 1997. Identification guide to North American birds. Part 1. Slate Creek Press, Bolinas, California.

Rusch, D.A.; Reeder, W.G. 1978. Population ecology of Alberta red squirrels. Ecology 59: 400–420.

Schmitz, O.J.; Sinclair, A.R.E. 1997. Rethinking the role of deer in forest ecosystem dynamics. Pages 201–223 *in* W.J. McShea, H.B. Underwood, and J.H. Rappole (eds.), The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C.

Sealey, S.G. 1974. Ecological segregation of Swainson's and Hermit thrushes on Langara Island, British Columbia. Condor 76: 350–351.

Sieving, K.; Willson, M.F. 1998. Nest predation and avian species diversity in northwestern forest understory. Ecology 79: 2391–2402.

Simes, R.J. 1986. An improved Bonferroni procedure for multiple tests of significance. Biometrika 73: 751–754.

Sipura, M. 1999. Tritrophic interactions: willows, herbivorous insects and insectivorous birds. Oecologia 121: 537–545.

Strauss, S.Y. 1991. Indirect effects in community ecology: their definition, study and importance. Trends Ecol. Evol. 6: 206–210.

Vila, B.; Vourc'h, G.; Martin, J.-L.; Guibal, F. 2002. Is escaping deer browse just a matter of time in *Picea sitchensis*? A chemical and dendroecological approach. Trees – Struct. Funct. 16: 488–496.

Restoration: Potential and challenges

Caption: Three pairs of pictures showing the same sites before and 8 years after the cull on Reef Island
Credit: RGIS, Jean-Louis Martin

Reduction in deer numbers on Reef Island and SGang Gwaay: progress, results, and vegetation changes

Anthony J. Gaston, Sean Sharpe, Stephen A. Stockton, Todd Golumbia, and Jean-Louis Martin

Abstract

To understand the effects on vegetation of a reduction in deer numbers, we removed deer and monitored the recovery of the vegetation on Reef Island and SGang Gwaay, Haida Gwaii (Queen Charlotte Islands, British Columbia). These two islands were chosen for their offshore isolation and lower colonization potential. The initial deer populations were estimated at fewer than 90 on Reef Island and fewer than 50 on SGang Gwaay. The islands were rugged, with abundant hiding and escape terrain. We tried several methods of deer removal, including baiting, hunting, and self-applying radio collars. The most successful method was hunting with hunters familiar with the local terrain. From the fall of 1997 to the fall of 2003, 85 deer were shot on Reef Island (>75% killed in year one) and 59 on SGang Gwaay (>80% killed in year one). The sex ratio of deer killed on SGang Gwaay during the initial culls was highly skewed to does (3:1), but it was not significantly different from 1:1 for Reef Island. On Reef Island and SGang Gwaay, only 36% and 28% of females, respectively, were pregnant or showed signs of lactating. The incidence of disease and parasites was exceptionally low, and obvious morphological deformities were very limited, but we found signs of nutritional stress. Males were generally in poorer condition than females. By 2001, fewer than five deer were estimated to remain on Reef Island, possibly a few more on SGang Gwaay.

We monitored vegetation changes by recording species presence and measuring vegetation cover by height strata in both interior and shoreline plots. Between 1997 and 2001, vegetation cover increased in all strata below the browse line, in shoreline and interior plots. The effect was greatest in the lowest strata. At Reef Island, the greatest proportional expansion occurred for red huckleberry *Vaccinium parvifolium*, false azalea *Menziesia ferruginea*, and salal *Gaultheria shallon*, all of which were still present initially as mature shrubs over most of the island. Species richness at Reef Island increased from 17 to 24 in interior plots and from 29 to 43 in shoreline plots. No new species were recorded in the 3.6-m plots at SGang Gwaay, but the mean number of species per plot increased from three to four for interior plots and from four to nine for shoreline plots. Exotics either remained stable (thistle *Cirsium* spp.) or decreased (stinging nettle *Urtica dioica*). Although the rate of expansion of western hemlock *Tsuga heterophylla* and Sitka spruce *Picea sitchensis*, which dominated the understory initially, was slower than that of the broad-leaved shrubs, their abundance may cause them to crowd out competitors soon, possibly reversing current increases in biodiversity. The process of vegetation recovery has only just begun, and the final shape of interior plant communities, if deer browsing continues to be restrained, cannot be determined. We urge that the Reef Island and SGang Gwaay experiments be extended to allow the vegetation to return to a deer-free configuration. For this, periodic culls will be necessary to prevent rapid return to precull levels.

1. Introduction

The substantial modifications that have taken place in the vegetation of almost every island in the Haida Gwaii archipelago (Queen Charlotte Islands, British Columbia) as a result of Sitka black-tailed deer *Odocoileus hemionus sitkensis* browsing (Pojar 1999; papers in this volume) make it difficult to reconstruct what the flora may have been like prior to deer introduction and to predict what the trajectory of recovery might be if deer were to be reduced or eliminated.

To investigate the feasibility of culling as a management tool and the response of the vegetation to the elimination of deer, the Research Group on Introduced Species has attempted to eliminate, or at least drastically reduce, deer on two islands: Reef Island, in Laskeek Bay, and SGang Gwaay, near the southern tip of Gwaii Haanas. This experiment will also, in the longer term, provide information on changes in songbird populations when deer populations are reduced and provide protection of cultural and biological resources. The culls were carried out under permit from the B.C. Ministry of Water, Land and Air Protection.

Reef Island and SGang Gwaay represent, respectively, the relatively drier east coast and the very wet and exposed west coast of the archipelago. They were chosen for their isolation, on the assumption that future deer immigration would be restricted (but see Reimchen et al. this volume). Both are large enough to support typical old-growth interior forest, and both showed signs of intensive deer browsing. Deer were present on Reef Island for at least 40 years prior to the cull (Vila and Martin this volume) and have been known to occur on SGang Gwaay for at least 45 years (Columbia et al. this volume).

We used the initial cull to gather information on basic biology, body condition, and morphometrics of isolated island populations of Sitka black-tailed deer. We compared the vegetation of the cull islands with the vegetation of islands used as controls and with that of the small island sample used by Stockton (this volume). We analyzed evidence for vegetation changes following the reduction of deer and used this to speculate on the future trajectory of recovery in the absence of deer.

2. Methods

2.1 Study sites

The terrain on both islands is rugged and provided abundant hiding and escape terrain for the deer. Because of the relative isolation of these islands from the nearest source populations of deer, we assumed low recolonization potential (but see Reimchen et al. this volume). Both islands lack introduced squirrels.

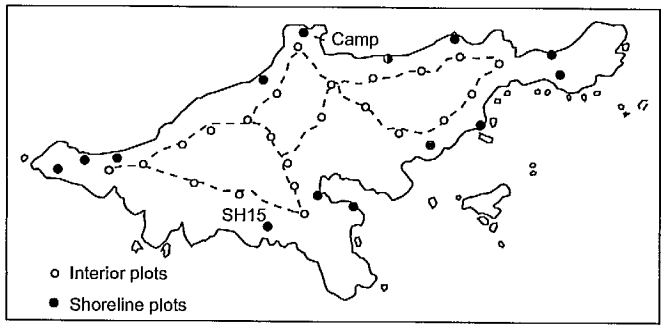
The vegetation on both Reef Island and SGang Gwaay consists of three major associations: 1) a mature western hemlock *Tsuga heterophylla*/Sitka spruce *Picea sitchensis* forest with scattered western redcedar *Thuja plicata*, with an open understory, except for scattered mature red huckleberry *Vaccinium parvifolium* and false azalea *Menziesia ferruginea* and patches of spruce or hemlock regeneration; 2) similar mature forest, but with dense salal *Gaultheria shallon* understory; and 3) open forest, mainly spruce, with a dense ground cover of Nootka reed-grass *Calamagrostis nootkaensis* tussocks.

2.1.1 Reef Island

Reef Island (Fig. 1) is 6 km from the nearest point of Louise Island, which is divided from Moresby Island by an artificial channel less than 100 m wide at the narrowest point. Louise Island is the most likely point of origin for deer immigrating to Reef Island.

Reef Island is 249 ha in area and rises to a maximum of 150 m above sea level. The ground rises steeply from the north coast to a ridge running approximately east–west along the long axis of the island. The ridge broadens into a dissected plateau in the centre of the island.

Figure 1
Map of Reef Island, showing the position of trails and permanent vegetation monitoring plots. SH15 is the shoreline plot unaffected by deer browsing.



Several major streams all drain towards two large coves on the south coast. The area in the vicinity of the coves is generally less steep than the north coast, but the southwest coast is very precipitous and lined with cliffs dissected by steep gorges. Several isolated stacks are more or less cut off from the main island.

On Reef Island, association 1 is found on almost all the north-facing parts of the island, as well as large parts of the interior plateau. Association 2 occurs on south-facing areas, both on parts of the interior plateau and especially on steeper slopes where the canopy cover is sparse. Association 3 is found predominantly on exposed ridges and headlands, especially at the east and west ends of the island.

Although no commercial logging has taken place on the island, there are several areas where disturbance has occurred within the past century. Around Camp Cove, on the north side of the island, an approximately 0.3-ha area of even-aged spruce, about 40 years old, probably marks the site of a former cultivation patch (Guujaw, pers. commun.). This may account for the continued presence of potato *Solanum tuberosum* on the island.

On the north slopes of the main ridge, towards the east end of the island, is a several-hectare area of even-aged spruce, perhaps 50–60 years old. There is some evidence that this area was burned at one time. In the centre of the island, just above Camp Cove and on the south side of the main ridge, a stand of tall, but not mature, hemlock is interspersed with scattered, very large spruce, mostly in an advanced state of decay. This area has clearly seen the replacement of spruce by hemlock over the past century.

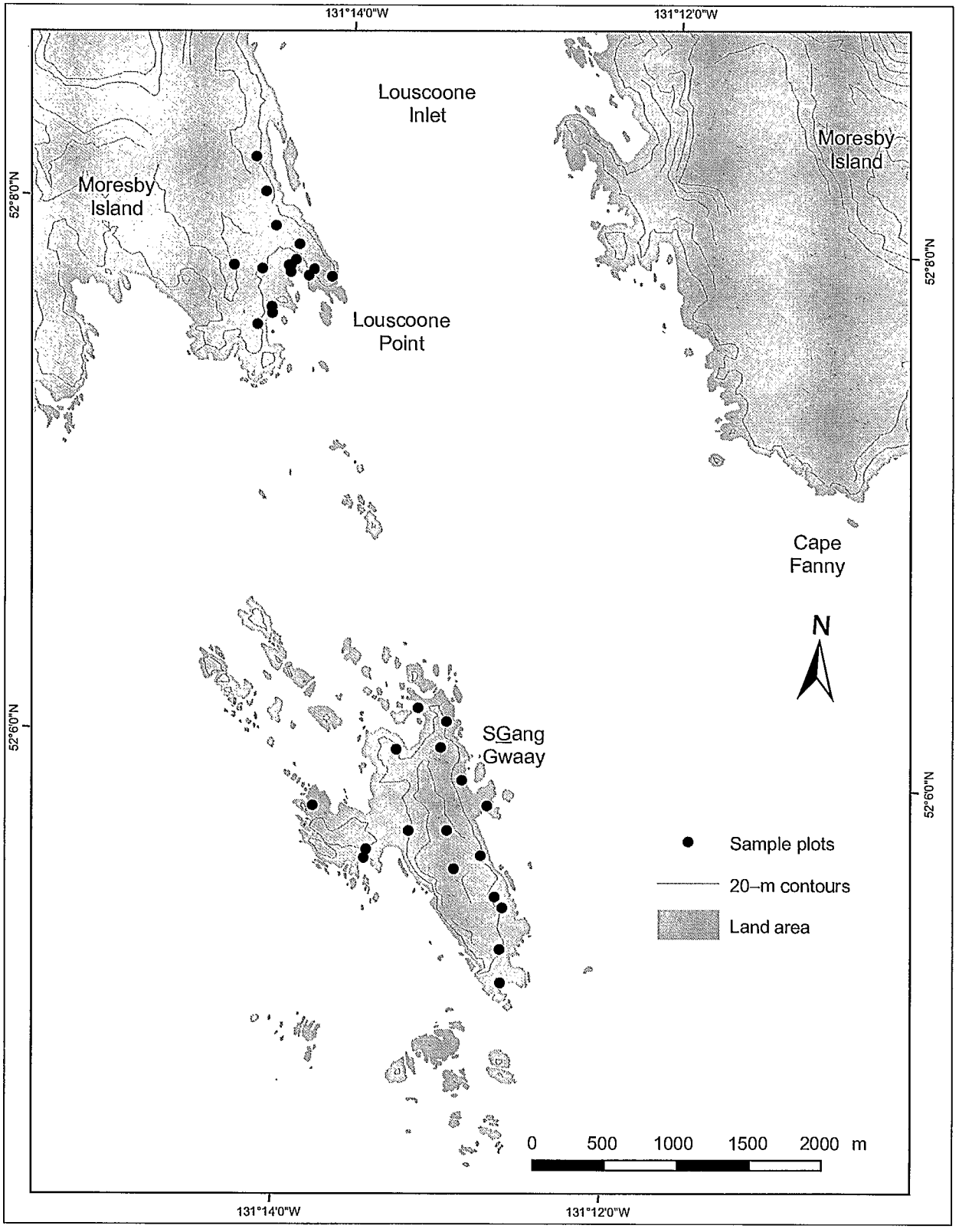
All of the main coves on the south coast have accumulated large quantities of driftwood above the high tide line, forming a barrier up to 10 m wide between the beach and the forest. These accumulations, consisting mainly of cut logs, cover up many areas that would otherwise support shifting storm beaches of boulder or gravel. This may exclude some plants of pioneer communities, while providing protection from grazing for some shrubs and flowers rooted inside the log barricade.

2.1.2 SGang Gwaay

The main island of SGang Gwaay (Fig. 2) is 135 ha in area, with 17 smaller islands and several rocky islets and reefs making up a total area of over 170 ha. Elevation does not exceed 30 m above sea level. SGang Gwaay is approximately 1.5 km from Moresby Island (Louscoone Point), the likely source of deer immigration. The main island is predominantly cedar–hemlock forest with a fringe of coastal spruce forest. The island is also recognized as a World Heritage Site and has considerable cultural resources in the old village site and throughout the extremely rugged island.

On SGang Gwaay, association 1 is found over most of the interior. Most of the terrain is undulating, with redcedar stands on higher ground and western hemlock/spruce in the valleys. Association 2 occurs in both northern and southern coastal draws under more open canopy. Association 3 is found predominantly on exposed ridges and headlands along the entire coast, but especially on the west. Several windfall areas where dense Sitka spruce is regenerating are found along the north and west coasts.

Figure 2
Map of SGang Gwaay, showing the position of permanent vegetation monitoring plots



No commercial logging has taken place on the island, although there is a large area of second-growth forest on the eastern half of the island where village residents cleared areas and gathered wood. The site of Ninstints village is located midway down the east coast of the island, where there are extensive remains of houses and poles, as well as cultivation areas. A Haida Watchman cabin is north of the village area, and, at the northeast end of the island, a small lagoon serves as a boat anchorage. Much of the island is extremely rugged, with rocky shores and limited coarse beaches. There are many rocky outcrops well inside the current treeline—evidence of relict shorelines.

2.2 Deer cull

In the initial efforts to cull deer, we attempted to prebait areas with a variety of food items, such as grains, apples, and fresh vegetable matter. Although some deer visited the bait stations, there was no significant concentration of animals, and the time, cost, and disturbance of setting up the stations were considered greater than the benefit of conditioning a limited number of deer to frequent the sites. The major effort to cull the deer was through a series of organized hunting parties in which groups of hunters worked sections of the island and drove deer towards constricted areas. Deer were shot when encountered. During summer and fall efforts, hunters also attempted to use fawn distress calls, doe calls, and antler rattling as techniques to draw deer out. Subsequent culls have taken place once or twice annually, resulting in only a few deer shot per subsequent and comparable cull effort. Due to the reduced efficiency of hunting, we also attempted to use self-administering radio collars (VHF transmitter attached to a loop of halibut fishing line and placed as a snare on a deer trail). The rationale was to use a radio-collared deer to track small groups of deer, particularly during the rut. Due to the lack of other large mammals on the study sites, there was no danger of nontarget species setting off the snares. We also made very limited use of lethal spring-loaded neck snares in a few locations where deer could be snared and killed quickly by breaking their necks. This was done to assess the potential of this approach in case a consensus was reached to use this method to maintain deer numbers at a low level in the absence of the resources needed for hunting.

2.3 Deer biology and use of meat

We recorded the weight and measured head length, total body length, hind leg length, shoulder height, and ear length on all deer culled during the initial hunts. We also recorded sex, body score, udder condition, and uterus/ovary condition. Mean body condition of deer was scored as a subjective rating between 1 (very poor condition) and 5 (excellent body condition). Indicators such as fat thickness on the back, fat thickness around internal organs, and evidence of backbone and ribs being visible were all used to score body condition of carcasses. We estimated pregnancy rates from fetus presence, signs of lactation, and ovary condition (recent placental scars or embryos), depending on the time of year that the deer were culled. We checked and collected samples of kidney fat, kidney, liver, rumen, mouth contents, and fecal samples. Parasites, disease, and deformities were noted when present. Additional tissue samples were collected for DNA microsatellite analysis. A tooth was collected for aging. Deer that were retrieved were butchered, and the meat was distributed through social services or consumed on site during the culls.

2.4 Vegetation monitoring

On Reef Island, interior vegetation was monitored in 23 study plots distributed at 200-m intervals and approximately 100–200 m inland, along a trail making a loop around the island periphery (Fig. 1). These points had been previously established for bird censuses (Martin et al. 1995). A second series of 15 plots (shoreline plots) was established 15 m inland from the seaward edge of the vegetation and scattered around the island to represent different types of shoreline (gravel, boulder, rock), aspect, and exposure. One plot (15, "hidden valley") was placed in a small cove cut off from the rest of the island by steep cliffs; no evidence of deer browse was found in this cove, and the vegetation is believed to represent that characteristic of sheltered coves on Reef Island prior to the arrival of deer.

On SGang Gwaay, 12 interior plots and 5 shoreline plots were established (Fig. 2), similarly to represent a range of habitat types across the island, being constrained mainly by the limited area of interior forest for interior plots. All plots were established on the main island. The same plots were used for bird point counts for long-term monitoring of songbird populations.

Each vegetation plot was circular and marked with a single central post. Interior plots were 25 m in radius, and shoreline plots 10 m. Within each interior plot, two 3.6-m-radius subplots were placed at 10 m north and south of the centre post and marked with permanent posts. For shoreline plots, a single 3.6-m subplot was centred on the same post as the 10-m plot. Within each 3.6-m subplot, intensive counts of seedling regeneration were made in a 1-m radius around the centre post.

For each plot, a species list was compiled by at least two (in some cases three or four) observers searching the entire area for about 10 minutes (longer if the area was densely vegetated). Species were identified according to Pojar and MacKinnon (1994) and Hitchcock and Cronquist (1991). Voucher specimens of all species were preserved and verified by comparison with collections maintained by Agriculture and Agri-Food Canada.

Canopy cover, shrub cover, and ground cover were estimated by strata (see Stockton this volume). Within each 3.6-m subplot, vegetation cover by stratum was recorded for each species. In addition, ground cover was estimated by categories (rock, litter, wood [>2.5 cm diameter], moss, water, bare ground). The cover estimates for the subplots were used to compile species lists for each.

Vegetation recording began in May 1997, and data were obtained from all study plots during June–July, before the initiation of the first deer cull in September of that year. Monitoring observations were made annually throughout the 5 years of the study (1997–2001), being repeated at

the same time of year (June through mid-July). Additional species found outside sampling plots were also recorded, although effort varied among habitat types. On Reef Island, a deliberate attempt was made to search steep cliffs and isolated stacks that might harbour deer-sensitive species.

2.5 Control sites

To control for possible ongoing changes in the vegetation of the archipelago as a whole, we selected control areas for comparison with changes at Reef Island and SGang Gwaay. The control areas were chosen for similarity of forest type, area, and topography. Kunga and East Limestone islands were selected as controls for Reef Island. Kunga Island, at the south end of Laskeek Bay, is larger (395 ha) and higher (420 m) than Reef Island, but similar in slope. East Limestone Island (41 ha) is smaller than Reef Island and lower (maximum 50 m). All three islands experience a rain shadow effect from nearby Louise and Moresby islands, making them somewhat drier than most of the archipelago. We selected 20 interior and 10 shoreline plots on Kunga Island and 10 interior and 9 shoreline plots on East Limestone Island. Vegetation monitoring at these sites was carried out using the same methods as on the treatment islands.

In the absence of nearby, similar islands to compare with SGang Gwaay, we selected the closest point on Moresby Island (Louscoone Point) for this purpose. Although similar in most biophysical aspects, this area appeared to have less browsing impact than the treatment island. On Louscoone Point, we selected 10 interior and 5 shoreline plots and carried out similar measurements as on the treatment islands. Due to logistical and time constraints, the initial measurements on Louscoone Point were delayed until 1998.

Results for species richness and similarity were also compared with those obtained by Stockton (this volume) for the small islands of Laskeek Bay where no deer are present (Low, South Low, and Lost islands). Sampling methods there were identical to those described for the cull islands.

2.6 Analysis

To give an overview of changes taking place in the vegetation since the initiation of deer culling, we have relied mainly on information from the 3.6-m subplots, because investigation of these subplots has been more intensive than for the 10-m and 25-m plots. We concentrated on changes in cover and species richness for different vegetation layers. Increases in cover were calculated as:

$$\text{Increase in cover} = [(C_{2001} / C_{1997}) - 1] \cdot 100\%$$

where C = mean cover (% plot area) of a given species in a given stratum on a given island, averaged over all plots.

As cover values were expressed as a percentage of the total area, the scope for increase was clearly greater for species that initially occupied only a small portion of the total area than for those initially covering most of the plot. For example, a plant covering 1% of the area initially that increased to 5% would experience a 400% increase in cover, whereas one that covered 50% initially could never increase more than 100%, although expanding over a much greater area.

Because species diversity and the proportion of cover in the various vegetation layers differ markedly between interior and shoreline plots, we analyzed these types of plot separately. Although monitoring observations were made each year, many comparisons present only the data for 1997 and 2001. This is because culling was progressive on both islands and substantial browsing continued through 1998, making the date at which browsing effects ceased rather imprecise.

3. Results

The first cull of deer on Reef Island occurred from 28 September to 3 October 1997, when 49 deer were killed. On SGang Gwaay, the first cull was made from 4 to 10 February 1998, when 19 deer were killed. On Reef Island, 73 animals were killed during four hunts spread between September 1997 and February 1999 (thus one breeding season). Subsequently, one (July 1999), five (June 2000), two (October 2001), two (February 2002, by lethal snares), and two (August 2003) animals were killed. As of October 2003, the cull efforts had resulted in the killing of 85 deer on Reef Island (37 bucks, 38 does, 10 unknown). On SGang Gwaay, 48 deer were killed in two hunts in 1998 (12 bucks, 32 does, 4 unknown). Another 11 (7 males, 4 females) were killed in September 2003, yielding a total of 59 deer killed. The sex ratio of deer killed during the initial culls was highly skewed to does (3:1)on SGang Gwaay, but it was not significantly different from 1:1 for deer killed on Reef Island.

By the summer of 2001, browsing had effectively been eliminated over practically the whole area, and it was estimated that fewer than five deer were left on Reef Island and possibly slightly more on SGang Gwaay.

3.1 Deer biology

Pregnancy rates of females were extremely low. On Reef Island, only 36% (10/28) were pregnant or had recent fawns, and only one case of possible twins was observed. On SGang Gwaay, only 28% (8/29) of females were pregnant or had fawns.

Assessment of carcasses indicated very low incidence of parasites and disease. On Reef Island, one animal had obvious external parasites, six had fibrous peritoneal nodules, four had liver lesions, two had calcified lung nodes, two had monorchid testes, and two had dimorphic testes. On SGang Gwaay, only one deer had external parasites, and two had liver lesions.

Although mean weight of deer did not differ significantly, SGang Gwaay does tended to be lighter on average than Reef Island does and bucks on either island (Fig. 3a). Measurements of total length indicated that both bucks and does killed on SGang Gwaay were smaller than those on Reef Island (Fig. 3b). In general, does appeared to

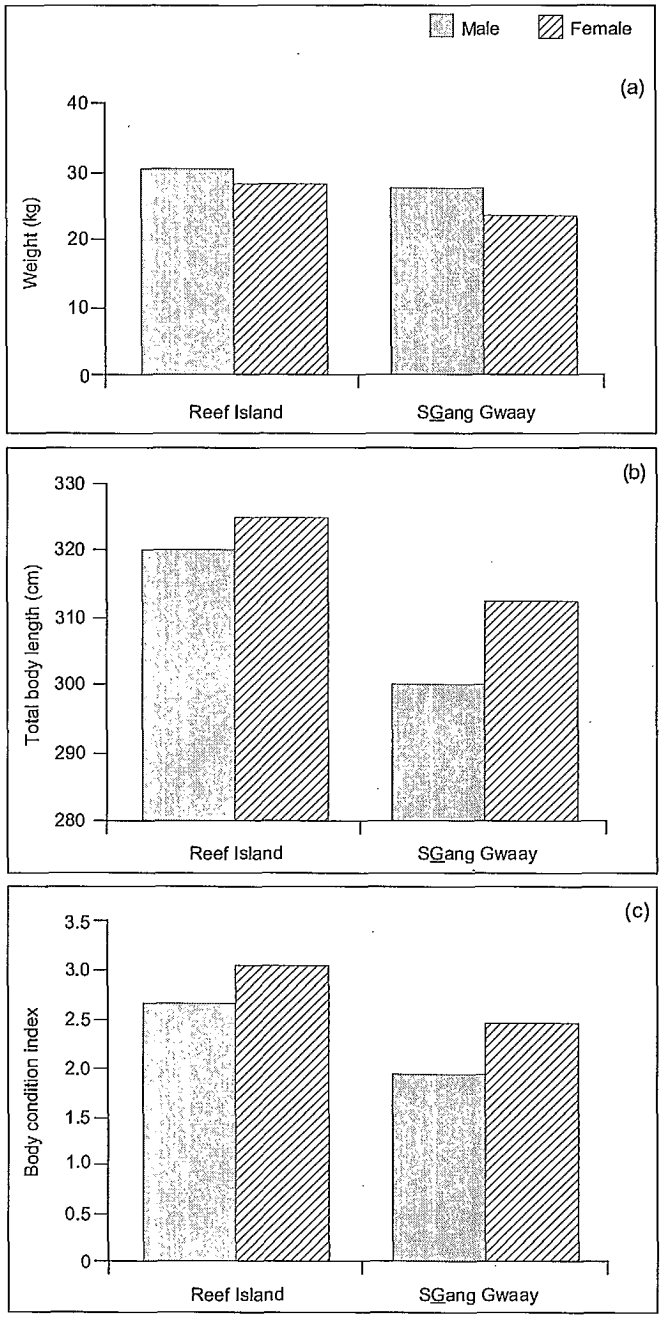
score somewhat higher in body condition index than bucks, and bucks from SGang Gwaay were in considerably poorer body condition than females. On average, deer on SGang Gwaay were in poorer body condition than Reef Island deer (Fig. 3c).

3.2 Species richness and floral similarities

We identified 135 species of vascular plants on Reef Island, out of a total of 164 species recorded on all the islands of Laskeek Bay (the "small island" sample of Stockton this volume, plus Kunga, East Limestone, and Reef islands). Another two species of exotic weeds were reported for Reef Island by Madrone Consultants Ltd. (unpubl. data), as well as four species elsewhere in Laskeek Bay. On East Limestone Island, 103 species have been recorded (Smith and Buttler 2000; Stockton, unpubl. data), on Kunga Island, 96 species, and on the aggregated "small islands" (Stockton, unpubl. data), 100 species (Table 1). A comparison of the species found on the Laskeek Bay islands showed that each was equally similar to the others: the flora of Reef Island was no more similar to those of Kunga and East Limestone islands than to those of the smaller islands (Table 1). In contrast, although the flora of SGang Gwaay was similar to that of the Laskeek Bay islands, that of Louscoone Point was quite distinct from all other areas in species composition, with 20 species (21%) found nowhere else, compared with 7–10% for all other sites.

When only interior plots were considered, the maximum number of species (68) was recorded at Reef Island. All but 1 of 19 species (95%) present at East Limestone Island, all but 1 of 23 species (96%) recorded at SGang Gwaay, all but 1 of 35 species (97%) present at Louscoone Point, and 26 of 29 (90%) species present at Kunga Island were also present at Reef Island. These comparisons suggest that as far as interior forests are concerned, the species composition differed little among islands, being a slightly varying subset of the same community.

Figure 3
Mean weight, total body length, and body condition of sampled deer on Reef Island and SGang Gwaay



3.3 Vegetation structure compared with control islands

The distributions of vegetation cover by height strata in interior plots on Reef Island in 1997 and on the two control islands (East Limestone and Kunga) resembled one another fairly closely, and the three islands had much lower cover values below 1.5 m than were found on the deer-free Low Island (Fig. 4a). For shoreline plots, cover in strata below 25 cm averaged higher at Reef Island than at the control islands and was similar to that on the deer-free island. However, cover at 0.5–1 m was much lower at Reef Island than on the deer-free island and similar to that on the control islands (Fig. 4b).

Vegetation cover in interior plots prior to the first cull was dominated by young Sitka spruce and western hemlock. This was especially true of the vertical strata between 0.5 m and the browse limit at 1.5 m, where these two trees comprised more than 80% of the initial cover (5–10% of area) on Reef Island (Fig. 5a).

Western hemlock was less abundant on SGang Gwaay, but both species dominate (>70%) all but the lowest and highest height classes in the sample plots (0–5 cm, 1.5–2 m, and 2–4 m) (Fig. 5b).

3.4 Changes to interior plots

Cover values increased between the initial (1997) and final (2001) measurements in all vegetation layers below the browse line (1.5 m), the effect being most striking close to the ground, where mean cover at 5–15 cm rose from 18% to 34% between 1997 and 2001 for Reef Island and from

Table 1
Species numbers and proportion of total flora for islands in northern Laskeek Bay, and indices of similarity among them

Island	Area (ha)	Total spp. recorded	% total for Laskeek Bay	Indices of similarity[a] East Limestone Island	"Small islands"	Kunga Island	SGang Gwaay	Louscoone Point
Reef Island	249	135	81	0.76	0.74	0.77	0.78	0.58
East Limestone Island	41	103	61		0.75	0.76	0.73	0.56
"Small islands"	62	100	60			0.74	0.71	0.53
Kunga Island	395	96	57				0.75	0.57
Laskeek Bay (total)	747	164						
SGang Gwaay	135	102	–					0.63
Louscoone Point (Moresby Island)	–	94	–					
Southern Region (total)	–	122						

[a] Index of similarity was calculated as $2N / (a + b)$, where N = number of species shared by the two islands, and a and b are the total number of species recorded on each island. The index varies from 0 (no species in common) to 1 (all species found on both islands).

Figure 4
Vegetation cover in four height strata (0–5, 15–25, 50–100, and 150–200 cm) in 3.6-m plots at deer cull (Reef Island, SGang Gwaay) and control sites (East Limestone Island, Kunga Island, and Louscoone Point) and at the deer-free Low Island, prior to deer culling: (a) interior, (b) shoreline

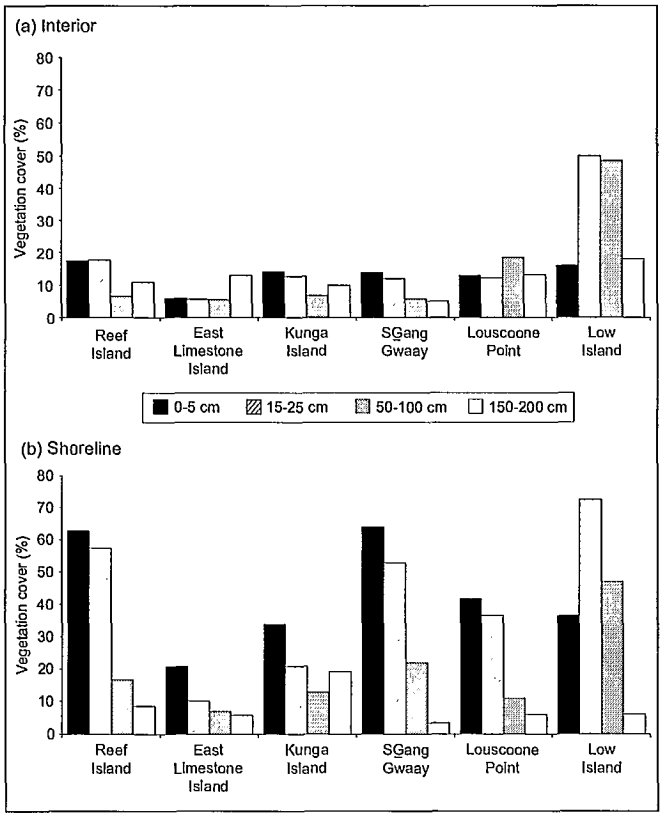
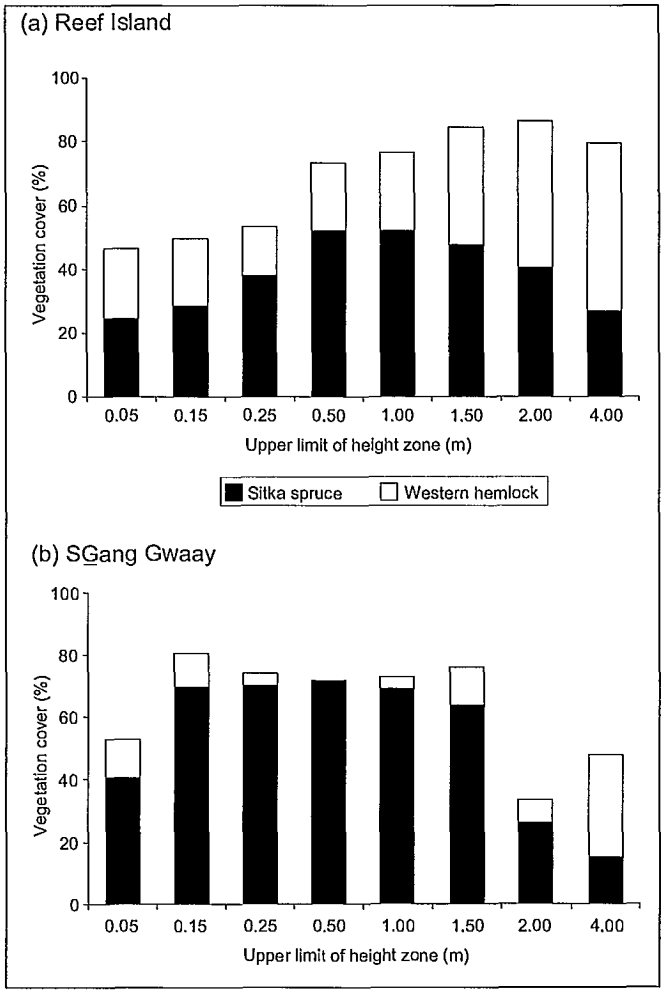


Figure 5
Representation of Sitka spruce and western hemlock in interior plots prior to the cull, as a percentage of total cover: (a) Reef Island and (b) SGang Gwaay



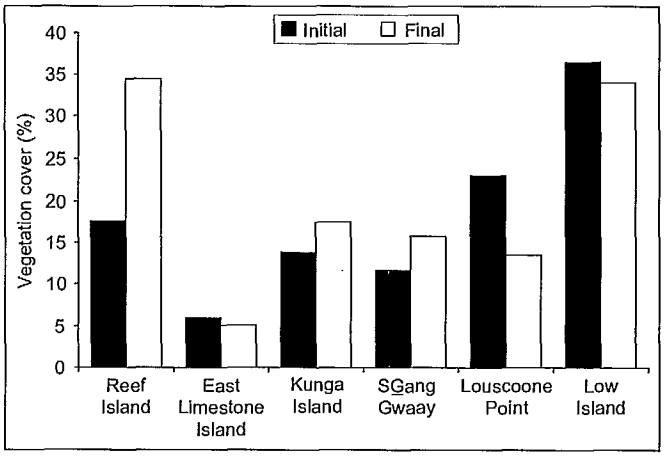
12% to 16% on SGang Gwaay over the same period (Fig. 6). No change comparable to that at Reef Island was seen at Kunga or East Limestone island, while a decrease in cover in this stratum from 23% to 13% was observed on Louscoone Point. Deer-free Low Island showed a slight decrease in cover.

Considering only species averaging >0.5% cover in 1997, the greatest percent increases in cover on Reef Island at 0–5 cm occurred for shrubs: false azalea, salal, salmonberry *Rubus spectabilis*, and red huckleberry, all of which increased in cover by more than 300% (Fig. 7a). The only other species to increase by >300% was the sword fern *Polystichum munitum*. Increases were similar in the 5- to 15-cm and 15- to 25-cm strata, with the addition of spiny wood fern *Dryopteris expansa*, which showed a roughly 500% increase in both strata. Red huckleberry showed the greatest increase in the stratum above 50 cm (nearly 2000%), where it was virtually absent in 1997. This shrub was present in 1997 as remnant overmature individuals, and some of the increase in cover in this stratum represents shooting from the base of elderly stems (see Vila and Martin this volume). Western hemlock and Sitka spruce showed lower increases in cover in all strata (above 5 cm, <150%). Nootka reed-grass showed slight decreases in all strata except 50–100 cm.

Although more subdued on SGang Gwaay, increases in vegetation cover exceeding 300% were detected for false azalea in the 5- to 15-cm stratum and for red huckleberry and salal at all heights. Deer fern *Blechnum spicant* showed increases of up to 150% in strata below 25 cm, while western hemlock increased by 400% above 50 cm (Fig. 7b). Minor decreases in reed-grass cover were evident in all strata.

At Reef Island, the total number of species recorded in 3.6-m plots rose from 17 to 24 between 1997 and 2001, with black gooseberry *Ribes lacustre*, red elderberry *Sambucus racemosa*, thimbleberry *Rubus parviflorus*, trailing blackcurrant *Ribes laxiflorum*, crisp sandwort *Stellaria crispa*, deer fern, and woodrush *Luzula* spp. added. No new species were detected in the plots on SGang Gwaay.

Figure 6
Vegetation cover in the 5- to 15-cm stratum in interior plots at Reef Island and SGang Gwaay for 1997 to 2001, with initial (1997) and final (2001) data from control islands for comparison



At Reef Island, mean numbers of species recorded at different heights on each plot rose by one (from three to four species) in the lowest height stratum and by nearly two species between 5 and 25 cm above the ground (Fig. 8a). On SGang Gwaay, the average change in species richness in 3.6-m plots ranged among strata from 0.2 to 0.6 species per plot (Fig. 8b). Changes above 1.5 m were negligible on both islands, although very few species occur in this stratum, in any case.

3.5 Changes to shoreline plots

Only a small increase in the vegetation cover in the 5- to 15-cm stratum was recorded at Reef Island from 1997 to 2001. The small change probably relates to the fact that this stratum was densely vegetated at the outset, supporting extensive grass cover. Nootka reed-grass covered 47% of the lowest height stratum in 1997: 76% of total cover for that stratum. Cover values at the two control islands, where reed-grass is much less common, were much lower and did not change during 1997–2001 (Fig. 9). SGang Gwaay showed a slightly larger increase, from 54% to 79%. Similar to the interior control sites, shoreline plots on Louscoone Point indicated a decrease in vegetation cover from 40% to 36%.

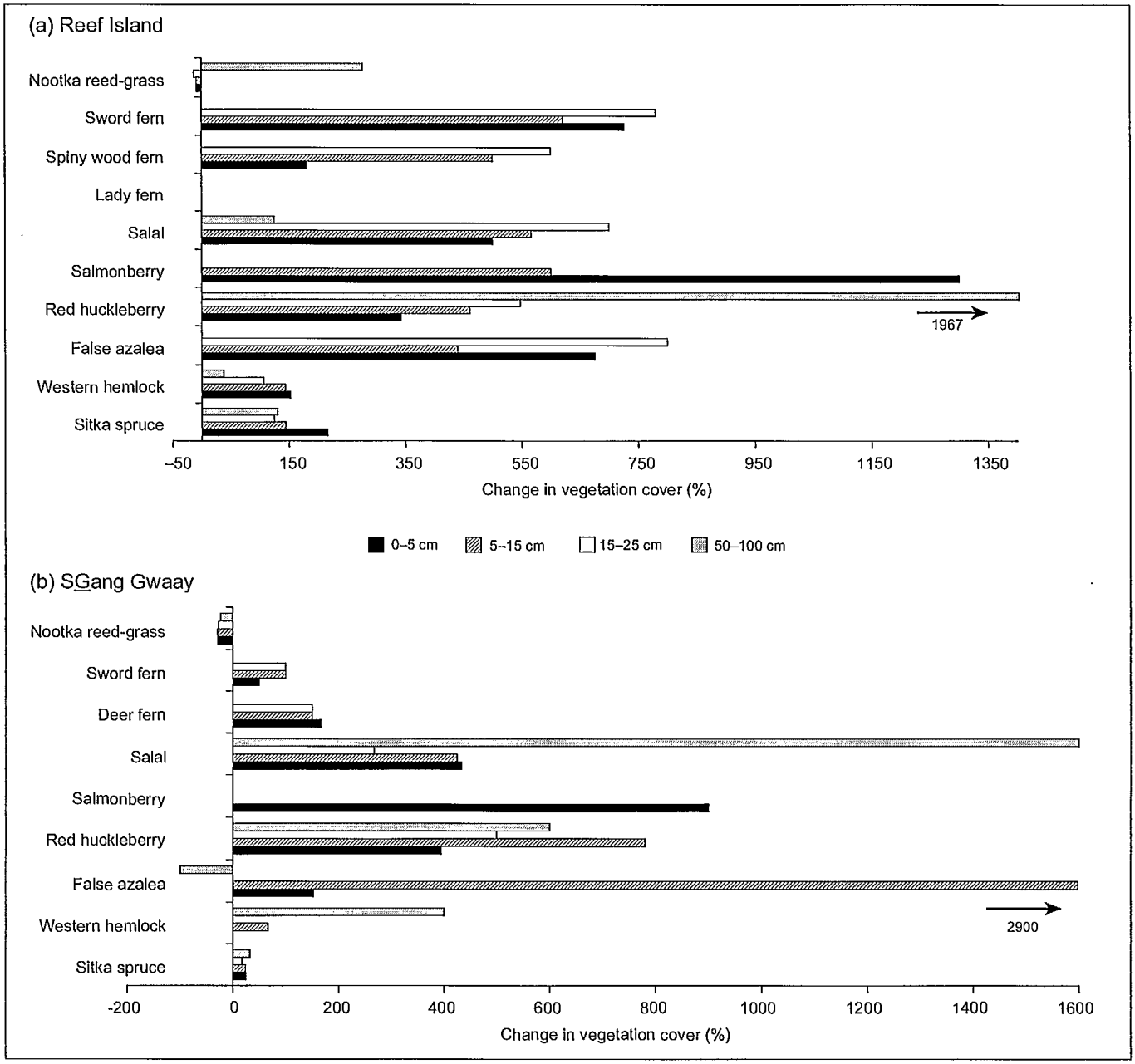
At Reef Island, shrubs showed the greatest increases in cover during 1997–2001, with salal, red huckleberry, and black twinberry *Lonicera involucrata* all showing increases of >300% in the 0- to 5-cm and 5- to 15-cm strata (Fig. 10). Similar increases were observed for sword fern and common harebell *Campanula rotundifolia*. Red huckleberry showed an even larger increase (>1000%) in the 15- to 25-cm stratum. Shore pine *Pinus contorta* increased by >200% in all strata below 1.5 m, showing a much greater increase than spruce (Fig. 11). Cover of western hemlock decreased in all strata below 1 m, the only species to show a consistent decrease in extent. Bull thistle *Cirsium vulgare*, present in five plots in 1997, did not expand. Nootka reed-grass increased somewhat in height, but not in extent, and the increase in sedges *Carex* spp. was small.

On SGang Gwaay, changes were observed in fewer species. Salal and dunegrass *Elymus mollis* showed large increases. Sitka spruce and Nootka reed-grass increased substantially only above 50 cm, while common yarrow *Achillea millefolium*, red huckleberry, and false azalea showed small increases in the lowest strata (Figs. 12 and 13).

On Reef Island, we identified 29 species in the 3.6-m plots in 1997, with an average of 4.4 spp./plot in plots 1–14: 15 species were found in plot 15 ("hidden valley"), including 7 species not found in any other plot. An additional 15 species were found in plots 1–14 by 2001, of which the most widespread were dunegrass (7 plots), western rattlesnake-root *Prenanthes alata* (6 plots), and western hemlock-parsley *Conioselinum pacificum* (4 plots). No species had disappeared from any plot. The average number of species per plot rose from 4 to 9 in the lowest vegetation stratum and from 3 to 5 in the 25- to 50-cm stratum: little change occurred in strata above 1.5 m (Fig. 14a).

Fourteen species were identified in shoreline plots at SGang Gwaay in both 1997 and 2001, with no new species observed between years. The average number of species per plot showed limited increases in the strata up to the browse

Figure 7
Increase in cover values at (a) Reef Island and (b) SGang Gwaay from 1997 to 2001 in 3.6-m interior plots, by species, for four height strata: 0–5, 5–15, 15–25, and 50–100 cm



line: plus 0.8 species at the lowest level and 1.2 species at the 5- to 15-cm and 15- to 25-cm strata (Fig. 14b).

3.6 Changes outside of plots

A few changes to the vegetation of both islands were noted, but were not captured by our sample plots. Probably many more such changes have taken place:

- A patch of stinging nettles approximately 30 m² in extent was present close to the shore behind Boat Cove, on Reef Island, from at least 1984 onwards, in an area thought to have been cultivated at one time. After 1997, this clump was invaded by Cooley's hedgenettle *Stachys colleyae*, so that by 2002, the stinging nettles had been almost completely replaced.
- Foamflower *Tiarella trifoliata* was not recorded at all on Reef Island in 1997. By the summer of 2001, it was common in the vicinity of camp and in many other places close to the shore. Although present (rarely) on SGang Gwaay prior to the cull, it was much more abundant and widespread on SGang Gwaay in subsequent years.
- On Reef Island, clasping twisted-stalk *Streptopus amplexifolius* was found near camp in 1999, and it has been seen with increasing frequency in this

Figure 8
Mean number of species per interior 3.6-m plot in 1997 and 2001 in relation to height stratum: (a) Reef Island and (b) SGang Gwaay

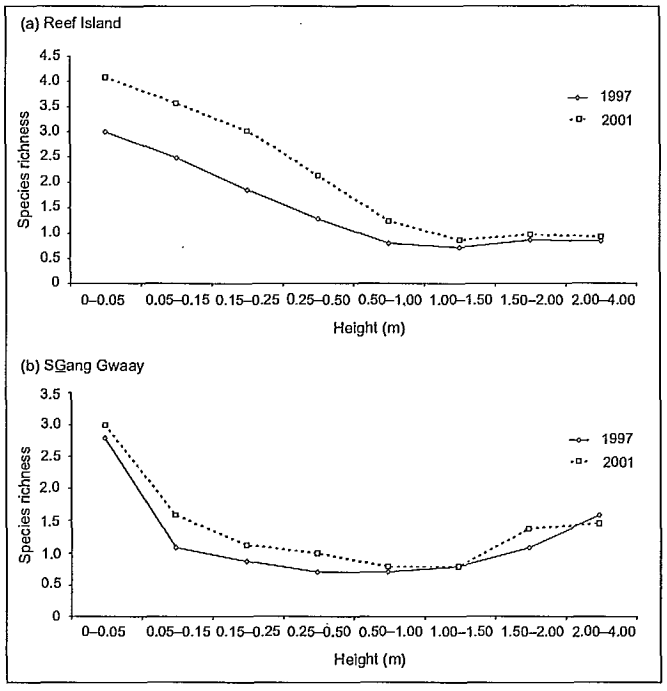


Figure 9
Vegetation cover in the 5- to 15-cm stratum in 3.6-m shoreline plots at Reef Island for 1997–2001, with initial (1997) and final (2001) data from control islands for comparison

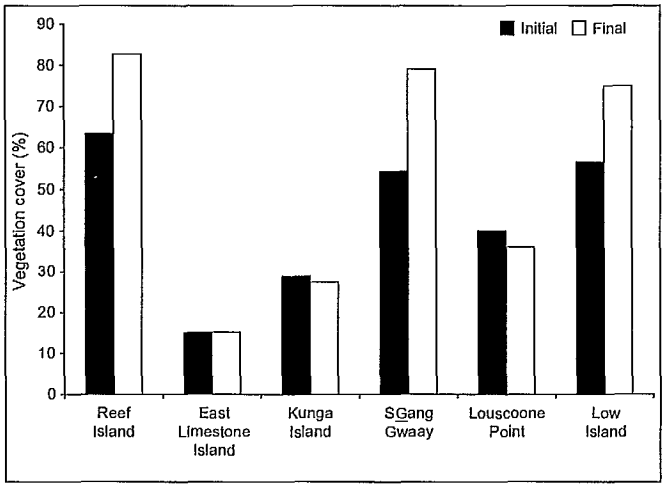


Figure 10
Increase in cover values at Reef Island from 1997 to 2001 in 3.6-m shoreline plots, by species, for four height strata: 0–5 cm, 5–15 cm, 15–25 cm, and 50–100 cm

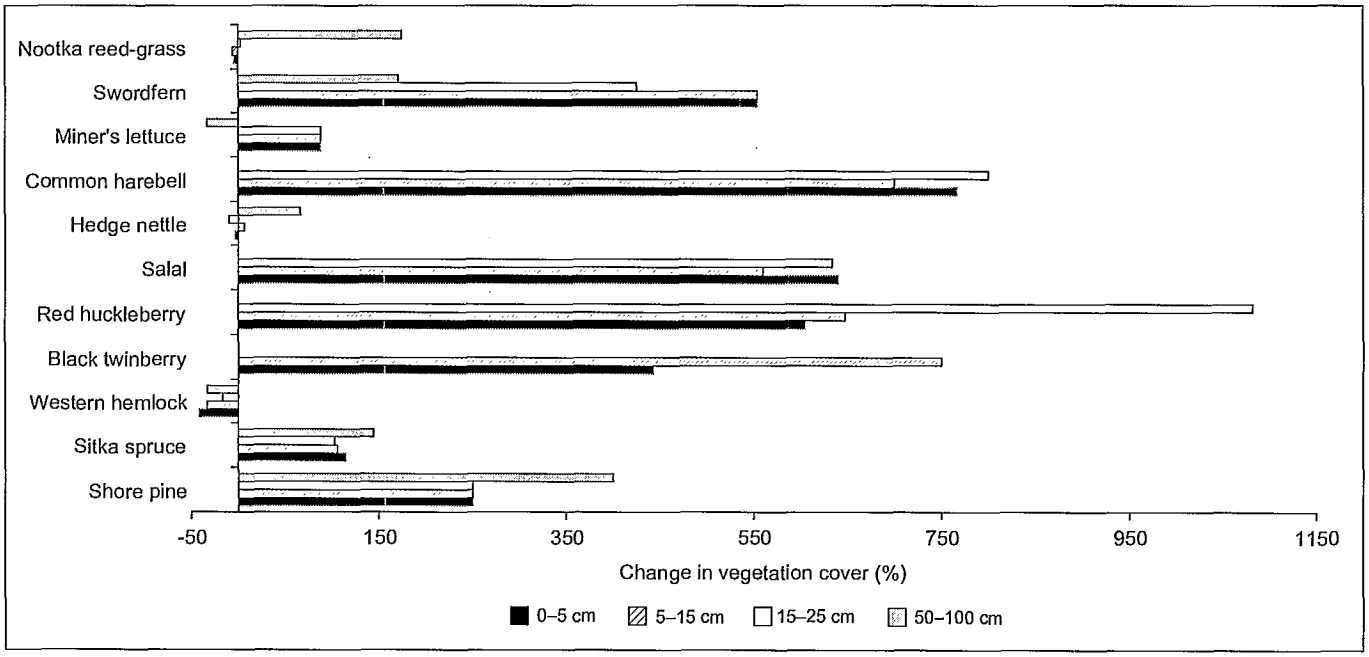
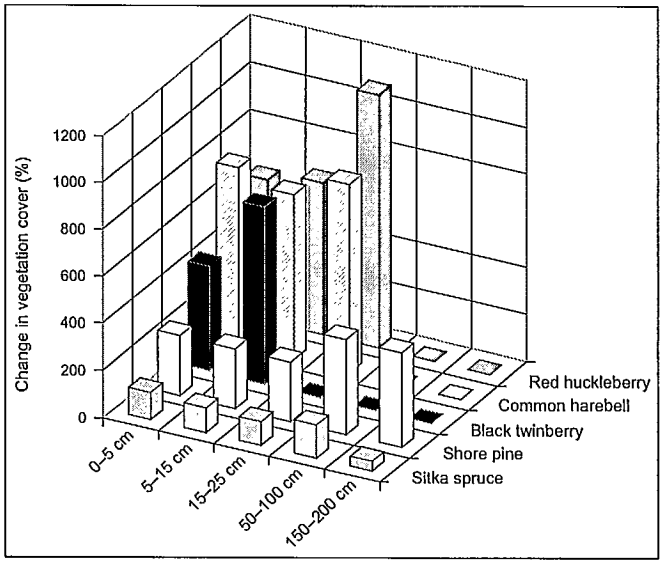


Figure 11
Increase in cover by height strata for Sitka spruce, shore pine, black twinberry, common harebell, and red huckleberry: Reef Island, 1997–2001, 3.6-m shoreline plots



level, heavily shaded area since then. It was not recorded at Reef Island prior to 1999. This species was also much more abundant and widespread on SGang Gwaay following deer reduction.

- In 1984, skunk cabbage *Lysichiton americanum* was present in a small swamp in the centre of Reef Island (Gaston, pers. obs.). This plant disappeared before 1988, and the species was not recorded on the island in 1997. However, by 1999, several small skunk cabbages were sprouting in the same area, and the species is now firmly reestablished. At SGang Gwaay, this species appeared in practically every wet area soon after browse pressure was reduced.
- In 1997, steep grassy slopes of nearly solid Nootka reed-grass occurred over broad ranges of Reef Island. In 1999, little or no change had occurred to these, but by 2000, small individuals of sword fern occurred in abundance within the grass. By 2002, the grass had been overtopped by the sword fern in several large areas (1–2 ha) on the south side of the island.
- In 2002, young redcedar seedlings or small saplings had become common, especially on Reef Island.

Figure 12
Increase in cover values at SGang Gwaay from 1997 to 2001 in 3.6-m shoreline plots, by species, for four height strata: 0–5 cm, 5–15 cm, 15–25 cm, and 50–100 cm

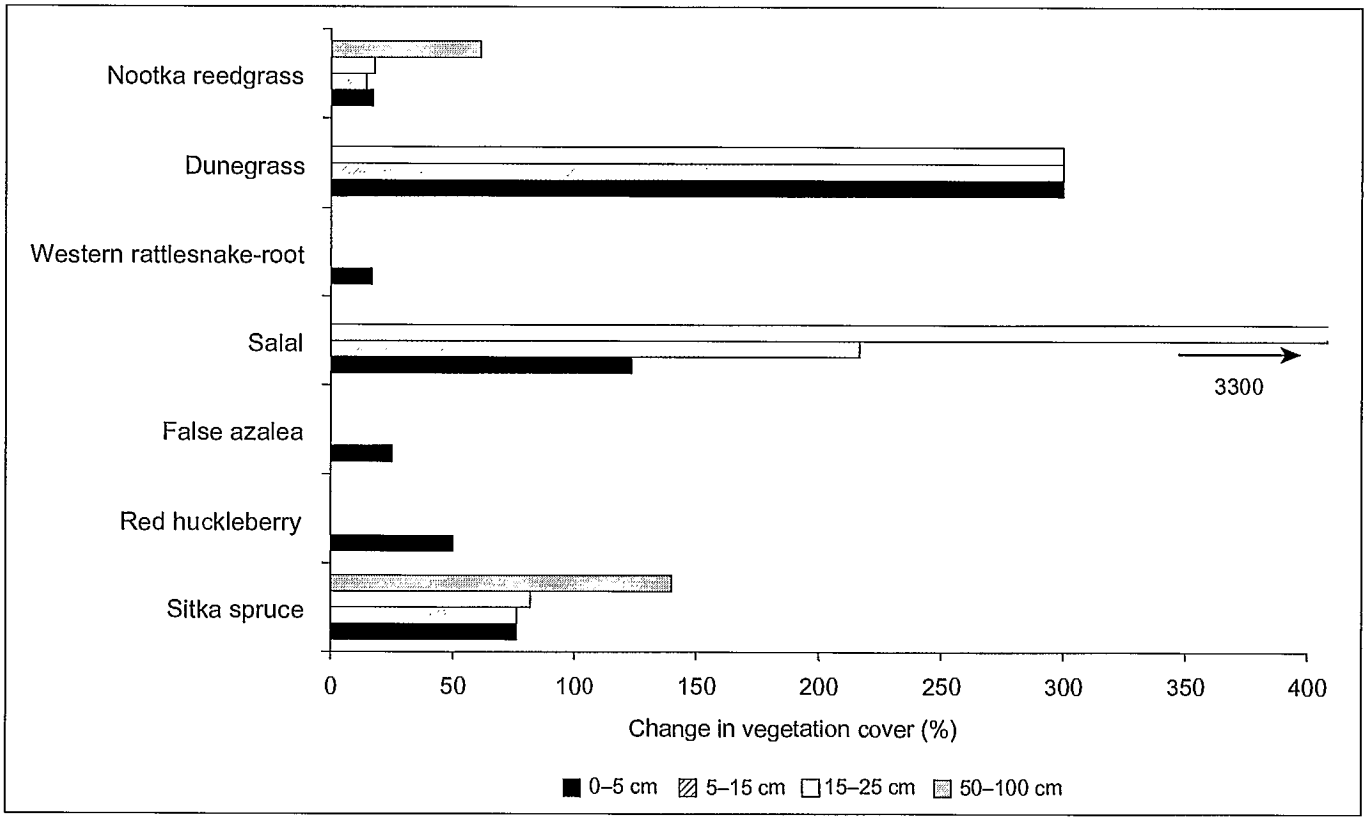


Figure 13
Increase in cover by height strata for Sitka spruce, red huckleberry, false azalea, salal, common yarrow, dunegrass, and Nootka reed-grass: SGang Gwaay, 1997–2001, 3.6-m shoreline plots

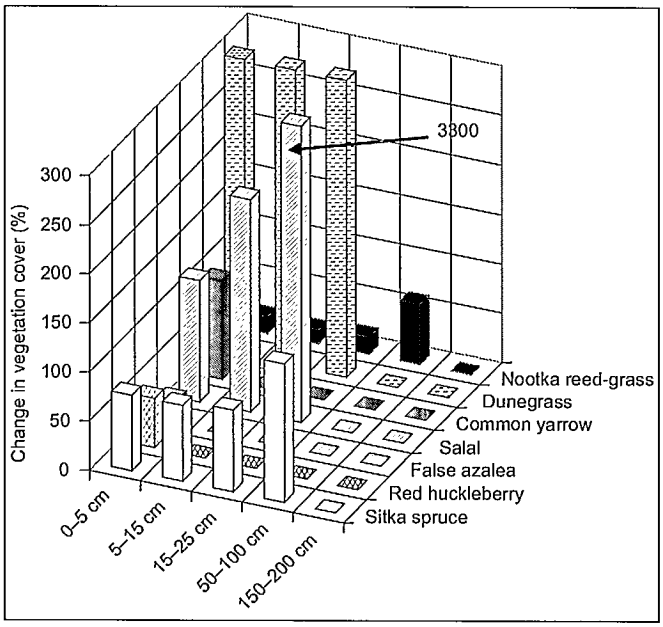
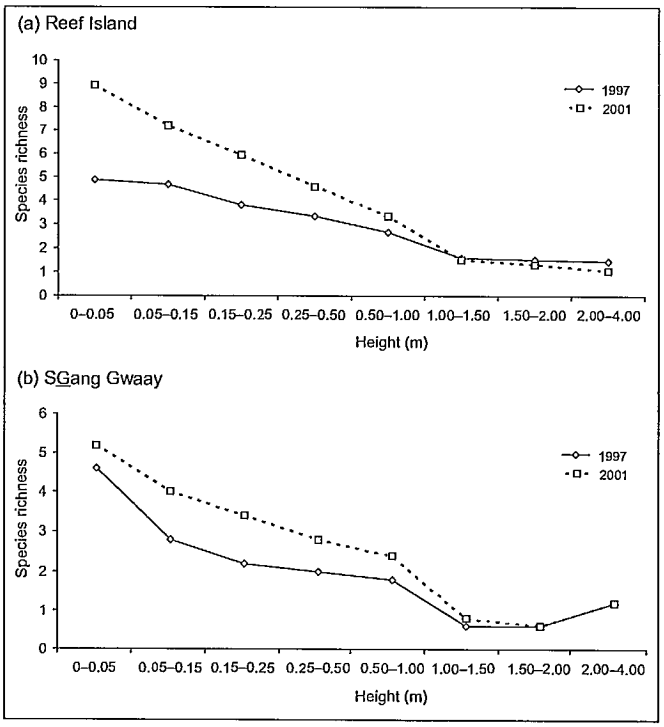


Figure 14
Mean number of species per 3.6-m shoreline plot in relation to height stratum for (a) Reef Island and (b) SGang Gwaay, in 1997 and 2001



4. Discussion

4.1 Deer cull

Hunting was a very effective way to reduce deer densities on the medium-sized islands selected. Although complete eradication of deer was desired, other means, such as lethal snares or highly trained dogs driving deer towards the hunters, may be necessary to kill the few remaining deer in a cost-effective manner and achieve complete eradication. The main interest of achieving complete eradication would be in being able to verify the results of Reimchen et al. (this volume) predicting rapid recolonization. Based on the results thus far, we would recommend that culls be conducted every second year or yearly, if feasible, to maintain deer at low densities, even if such a rate reduces hunter success per unit effort. Although too frequent human activity may reduce the effectiveness of hunting as a culling tool, low success per unit effort is also the inevitable consequence of success in maintaining deer population low and thus of achieving habitat recovery. The most effective approach to hunting, so far, was the use of hunting parties of 4–6 people working together in a systematic fashion in physically discrete quadrats of the islands.

The low pregnancy and fawning rates and low incidence of twinning in the deer killed during the initial hunts may indicate that deer on both islands were subjected to substantial stresses. This is further corroborated by the body condition indices and sex ratios on SGang Gwaay. The very low incidence of disease and parasites is consistent with the introduction of deer in the absence of predators and alternative parasite hosts. The low incidence of evidence of inbreeding deformities corroborates the results of Reimchen et al. (this volume) that indicated multiple and ongoing colonization events.

The population sizes estimated for each island after the initial culls (75–80 deer on Reef Island, 50–55 on SGang Gwaay; about 30 deer/km^2 in both cases) were consistent with the density estimates obtained for Reef Island and nearby East Limestone Island prior to the cull in 1996 (32.5 deer/km^2; Daufresne and Martin 1997).

4.2 Vegetation trajectory so far

Compared with the deer-free islands studied by Stockton (this volume), Reef Island, SGang Gwaay, and the control sites had a much more open understory before the initiation of the cull, especially in the island interior. Our time series of observations on Reef Island confirmed many of the effects inferred from cross-sectional studies of the smaller islands of Laskeek Bay (Stockton this volume). The rapid recovery of shrubs in both interior and shoreline zones suggests that in a deer-free state, Reef Island would support a much denser understory than at present. In addition, our observations suggest that biodiversity at all scales has been substantially depressed by deer browsing. Whether the upsurge of diversity witnessed to date, during a phase when space is not limiting in the majority of study plots, will be maintained will be revealed only by future monitoring. However, the retreat of nettles, the reduction of western hemlock in the shoreline zone, and the lack of expansion

of thistles suggest that competition is already showing some effects on species previously at an advantage through unpalatability or browse-resistant structure.

On Reef Island, shoreline sites tended to have a much denser ground layer than on the two control islands, mainly because Reef Island supported more extensive reed-grass areas than either control island. The development of Nootka reed-grass tussocks on Reef Island was not paralleled on any other islands in Laskeek Bay, although it was found on a smaller scale on some exposed islands farther south. Similar dense reed-grass areas are found on some offshore islands on the west coast (e.g., Helgesen Island, SGang Gwaay; Gaston and Stockton, pers. obs.): this feature may be related to exposure. Consequently, vegetation changes at Reef Island are not likely to exactly match changes that might take place on more inshore islands.

On the small islet off the southeast coast of Reef Island (apparently rarely visited by deer) and on deer-free Low Island, shrubs cover areas topographically similar to those supporting reed-grass on Reef Island. This suggests that deer may have had some role in maintaining the reed-grass association on Reef Island. The observation that sword fern is beginning to invade some reed-grass areas hints that without deer, reed-grass may become a less prominent feature on Reef Island.

Because the reduction of deer on Reef Island took place over several years, we cannot look on the changes observed between 1997 and 2001 as illustrating 5 years of recovery. Similarly, slower recovery on SGang Gwaay may also be related to the slightly less thorough and shorter duration of browse reduction compared with Reef Island. Changes in browse pressure observed in the study plots and in other areas appear to have been progressive. Observations at Reef Island in 1998 suggested that deer browsing in the previous winter had been heavy in places but light or nonexistent in others, perhaps because deer withdrew from open areas after the culls. From the summer of 1999 onwards, signs of browsing were sparse, and we believe that the density of deer from then onwards was less than 20% of initial density. This was sufficient to produce clear signs of vegetation recovery throughout the island, but some impact from deer has presumably continued. Hence, our results need to be viewed as evidence of vegetation response to heavy culling, rather than eradication, although by 2001 the deer population probably was less than five individuals, at least on Reef Island.

In terms of cover values, the understory shrubs that survived to 1997 within reach of deer—red huckleberry, false azalea, and salal—were the species that showed the most dramatic increases. These species retained stems and rootstocks that could develop rapidly as soon as browse pressure was released, expanding cover in all height strata. By contrast, species such as black twinberry, salmonberry, and Pacific crab apple *Malus fusca* increased mainly by seedling development, so that their share of cover increased more slowly and was concentrated in the lowest strata.

Species showing the most rapid expansion of cover are presumably those that were providing the main forage for deer during the spring. In contrast, those species that have shown little change in cover presumably represent either slow-growing species or ones that are less preferred by the deer. These include sedges, Nootka reed-grass, and western hemlock. Our observations support the previous suggestion that western hemlock regeneration benefits from suppression of other understory plants (Martin and Baltzinger 2002).

Only 75 species of plants were recorded on Reef Island in 1997, compared with a minimum of 135 now known to occur. Undoubtedly, 4 years of intensive investigation would have revealed additional species, even without deer culling. On the other hand, many new records were of conspicuous flowers or of plants close to heavily used areas near camp. The appearance of new species on the island is unlikely to have been caused by immigration. Low-growing plants, especially those with inconspicuous leaves, and flowers that were attractive to deer probably went unnoticed prior to the deer cull: this may have applied to twisted-stalk, scurvy grass *Cochlearia officinalis*, blue-eyed mary *Collinsia parviflora*, deer cabbage *Fauria crista-galli*, and foamflower, none of which was recorded in 1997.

Overall, SGang Gwaay showed a slower recovery than Reef Island. This is likely a result of several factors. SGang Gwaay was determined (albeit subjectively) to be less impacted than Reef Island at the beginning of the study, suggesting that the recovery would be less obvious at this site. Also, conditions on the west coast of the archipelago may cause poorer growth due to the higher degree of exposure to extreme weather (wind, rain, and cloud cover), as well as a poorer soil nutrient base. It is also possible that the forest presents a more closed canopy condition and therefore less available light for forest floor vegetation (Stockton 2003). Finally, the relative reduction in deer density might have been less severe on SGang Gwaay.

At the southern study area, we found that Louscoone Point (on Moresby Island) was less impacted than SGang Gwaay at the outset of the study and therefore anticipated that a decline in vegetation cover might occur over the period of the study. This was confirmed by our observations, which indicated that deer browsing in this area are still noticeably degrading the vegetation (see Vila and Martin this volume).

4.3 The future

Although we have observed many obvious vegetation changes in response to the deer cull, it is still too early to say what the eventual configuration of the vegetation will be without deer. It appears certain that the understory will increase, but what the final composition will be is still an open question. This is especially true for interior, north-facing areas, which are not duplicated on the small deer-free islands, with their rather open canopy.

Despite the rapid recovery of deciduous shrubs, we need to consider that young trees made up the bulk of the understory in the forest interior at the time of the cull, especially at above 50 cm from the ground. This head start may allow the young trees to close out competing shrubs, forming the type of dense regrowth that occurs after clearcutting. If this happens, the current increase in species diversity may be reversed for a period, until the dense young stands begin to thin out.

In addition, the reduction in browse pressure may affect the relative competitiveness of young canopy trees.

Already, spruce appears to be outcompeting hemlock, as it has expanded its cover more rapidly in strata below the browse line since culling began. If deer have been present at Reef Island for only 40–50 years (Vila and Martin this volume), then this is a relatively short window compared with the generation time of the forest trees. However, if recruitment during that period has been affected by deer browsing, we may see this imprint for many centuries in the composition of areas regenerating on recent blow-downs.

As yet, the Reef Island and SGang Gwaay projects remain very incomplete experiments. We have much to learn about the final configuration of the interior vegetation without deer: certainly decades of monitoring will be required. However, in October 2003, despite the best efforts of the hunters, there was still at least one deer left on Reef Island and more than one on SGang Gwaay. In addition, we now know from molecular genetics studies (Reimchen et al. this volume) that we have to expect regular immigration to the islands, although this is likely to be much less frequent than at inshore islands. These observations suggest that although we have a great opportunity for further research at Reef Island and SGang Gwaay, it will require additional investment in time and money over a considerable period, perhaps indefinitely, to bring these projects to proper fruition.

If we choose to make that investment, the value for research and for public education could be very great. Despite the mushrooming of deer exclosures on the main islands, the creation of island-size exclosures seems very unlikely. Moreover, no mainland site of comparable area is likely to embrace the same diversity of topography and vegetation types that can be found on these islands. Those of us who have been involved in the project, whether as researchers or as hunters, feel very enthused about the results to date. It is as though the arrow of time has become a boomerang, revealing progressively more of the islands' past. Although the research that has been conducted will endure, even if the deer are allowed to expand again, a great opportunity will have been lost if we walk away from the project now. We would like to see both islands become a permanent window on the history of the archipelago, available as an educational resource for islanders, researchers, students, and tourists. Those who know these islands know that they are very special places. They can become even more special if we find the resources to carry through what has come so far towards completion.

Acknowledgements

We thank all those who assisted in deer culling at Reef Island and SGang Gwaay: Brian Fuhr, Jason Goetzinger, Tim Hiltz, Ron Husband, Terry Husband, Rob Kelly, Kris May, Jack Richardson, Frank Shannon, Tom Smith, Charlotte Tarver, Steve Tennant, Andreas Uttendorfer, Bill Yovanovich, and Gwaii Haanas staff: Judson Brown, Anders Hawkins, Ron Leblanc, Grant Peregoodoff, and Renee Wissink. For work on the vegetation, we thank Christine Adkins, Liann Bobechko, Céline Boutin, Isabel Buttler, Denis Chrétien, Christine Eberl, Joëlle Fournier, Ian Fuhr, Rob Kelly, Jim Pojar, Barb Rowsell, and Nadine Wilson. The cull efforts would not have been possible without the skills and dedication of the local Haida Gwaii hunters. Veterinary services were provided by the B.C. provincial veterinarian, Helen Schwantze. Staff and other contributions in kind were provided by Parks Canada, B.C. Ministry of Water, Land and Air Protection, B.C. Ministry of Forests, and the Council of the Haida Nation.

Literature cited

Daufresne, T.; Martin, J.-L. 1997. Changes in vegetation structure and diversity in relation to the presence of a large herbivore: the impact of introduced black-tailed deer on old-growth forests in Haida Gwaii (Queen Charlotte Islands). Pages 2–26 *in* A.J. Gaston (ed.), Laskeek Bay Research 7. Laskeek Bay Conservation Society, Queen Charlotte City, B.C.

Hitchcock, C.L.; Cronquist, A. 1991. Flora of the Pacific Northwest. University of Washington Press, Seattle, Washington.

Martin, J.-L.; Baltzinger, C. 2002. Interaction among deer browsing, hunting, and tree regeneration. Can. J. For. Res. 32: 1254–1264.

Martin, J.-L.; Gaston, A.J.; Hitier, S. 1995. The effect of island size and isolation on old growth forest habitat and bird diversity in Gwaii Haanas (Queen Charlotte Islands, Canada). Oikos 72: 115–131.

Pojar, J. 1999. The effects of deer browsing on the plant life of Haida Gwaii. Pages 90–97 *in* G.G. Wiggins (ed.), Proceedings of the cedar symposium: growing western redcedar and yellow-cypress on the Queen Charlotte Islands/Haida Gwaii. B.C. Ministry of Forests/Canada–British Columbia South Moresby Forest Replacement Account, Victoria, B.C.

Pojar, J.; MacKinnon, A. 1994. Plants of coastal British Columbia, including Washington, Oregon and Alaska. Lone Pine Publishing, Vancouver, B.C.

Smith, J.L.; Buttler, I. 2000. First record of Menzies' pipsissewa, *Chaimaphila menziesii*, on Haida Gwaii. Page 29 *in* A.J. Gaston (ed.), Laskeek Bay Research 9. Laskeek Bay Conservation Society, Queen Charlotte City, B.C.

Stockton, S.A. 2003. The effect of introduced Sitka black-tailed deer, *Odocoileus hemionus sitkensis* Merriam, on the forest understorey plant communities of Haida Gwaii, British Columbia: pattern, process and recovery. Ph.D. thesis, University of Ottawa, Ottawa, Ontario.

Estimating deer colonization rates to offshore islands of Haida Gwaii using microsatellite markers

T.E. Reimchen, R.J. Nelson, and C.T. Smith

Abstract

Sitka black-tailed deer *Odocoileus hemionus sitkensis* were introduced to Haida Gwaii (Queen Charlotte Islands, British Columbia) in the late 1800s, after which they greatly increased in numbers and dispersed throughout the archipelago. In an attempt to reduce the major ecological impact of these introductions, deer populations were culled from two of the most remote of the islands, Reef Island and SGang Gwaay. We estimate here the colonization/dispersal rates of deer to each of these islands from the adjacent source islands, Louise and Moresby, through analysis of 10 microsatellite DNA markers in 141 deer. Eight of the loci surveyed had two alleles, whereas two loci had three alleles. Allelic diversity and allele frequencies were similar between SGang Gwaay and Moresby Island ($F_{st} = 0.1$, $P < 0.01$), between Reef and Louise islands ($F_{st} = 0.072$, $P < 0.01$), and between SGang Gwaay and Reef Island ($F_{st} = 0.079$, $P < 0.01$). N_em values derived from F_{st} values suggest that there are 2.23 migrants per generation between Moresby Island and SGang Gwaay and 3.22 migrants per generation between Louise Island and Reef Island, or approximately one individual per year. These high dispersal rates will reduce the efficacy of deer removal programs.

1. Introduction

One of the most widely distributed exotic species on Haida Gwaii (Queen Charlotte Islands, British Columbia) is the Sitka black-tailed deer *Odocoileus hemionus sitkensis*, which was introduced in the late 1800s, after which the species greatly increased in number and dispersed throughout much of the archipelago (Foster 1965; Carl and Guiget 1972). Two of the remote islands in the southern regions of the archipelago, Reef Island and SGang Gwaay, which contain deer, were chosen for a deer removal experiment and to evaluate the subsequent rate and extent of ecosystem recovery. Reef Island, located 6 km to the southeast of Louise Island, is one of the most distant of the small islands of the archipelago, while SGang Gwaay is located 2 km off the southern tip of Moresby Island but is separated by strong tidal currents. Deer dispersed to these islands by swimming, but the timing of their original colonization is currently unknown, although it probably occurred within the first five decades of their initial introduction to the large islands (Vila and Martin this volume). While mule deer *Odocoileus hemionus* are known to swim up to 25 km between islands in the Great Lakes, the remoteness of the oceanic islands and high current regime, usually with extensive surface wave action, suggest that there may have been only a single or a low number of colonization events.

In this paper, we take a genetic approach to estimating colonization/migration rates of deer to Reef Island and SGang Gwaay from the adjacent source islands, Louise and Moresby. Ten microsatellite DNA genetic markers were surveyed in samples from each of the locales and analyzed to determine to what degree the ocean distance separating the islands presents a barrier to migration.

2. Methods

As a result of culling during 1998 to 2000, tissue samples were obtained from 150 black-tailed deer from multiple sites on Haida Gwaii. Sixty deer were taken from Reef Island and 38 deer from SGang Gwaay. This was thought to comprise the majority (>90%) of the deer population on each island. Thirty-three deer were sampled on Louise Island, the most probable source population for migration of deer to Reef Island, and 19 deer were sampled on the south end of Moresby Island, the most probable source of animals colonizing SGang Gwaay.

2.1 Extraction of DNA, polymerase chain reaction, and electrophoretic conditions

Crude DNA extracts were prepared from liver tissue according to the method of Nelson et al. (1998). Each 25-µL polymerase chain reaction (PCR) required 1 µL of crude extract. We collected genotypic data for 10 microsatellite DNA loci. All loci are listed along with PCR annealing temperatures and gel electrophoresis times in Table 1. An MJ PTC-100 thermal cycler (MJ Research, Watertown, Massachusetts) was used to carry out PCR in 96-well microtitre plates; each reaction of 25 µL contained 10 pmol (0.4 µM) of each primer, 80 µM of each nucleotide, 20 mM Tris pH 8.8, 2 mM $MgSO_4$, 10 mM KCl, 0.1% Triton X-100, 10 mM $(NH_4)SO_4$, and 0.1 mg/mL bovine serum albumin. After a 3-minute incubation at 94°C, PCR mixtures were held at 80°C while 1 unit of Taq DNA polymerase was added, following which

Table 1
Annealing temperature and electrophoresis run time for deer microsatellite DNA loci

Locus	Annealing temperature (°C)	Run time (hours)	Reference
ILSTS001	50	15	Kemp et al. 1995
Cervid1	50	18	DeWoody et al. 1995
OarJMP12	50	15	Lumsden et al. 1996
ILSTS52	52	18	Kemp et al. 1995
ILSTS65	52	15	Kemp et al. 1995
T193	55	18	Jones et al. 2002
DeerC273	55	15	Jones et al. 2002
DeerC89	50	15	Jones et al. 2000
DeerT7	48	18	Jones et al. 2000
DeerT32	57	18	Jones et al. 2000

temperature cycling was initiated. Both the denaturation and extension PCR steps were for 30 seconds at 94°C and 72°C, respectively. Following amplification, 3 µL of 10X loading dye (50 mM EDTA pH 8.0, 30% glycerol, 0.25% bromphenol blue) was added to each reaction, and 10 µL of this solution was loaded per gel electrophoresis lane.

Microsatellite alleles were size-fractionated on nondenaturing polyacrylamide gels 17 cm wide by 14.5 cm long, containing acrylamide to bis-acrylamide in a 19:1 ratio to a total acrylamide concentration of 10%. Gels contained 2X TAE buffer (Sambrook et al. 1989), as did the running buffer. Each gel included three 20 base pair marker (GenSura Labs Inc., Del Mar, California) lanes to create a molecular size grid and 24 individual deer samples. Gels were stained with 0.5 µg/mL ethidium bromide in water and visualized with ultraviolet light. Digital images of gels were obtained with an Eagle Eye system (Stratagene Corp., San Diego, California). Gels were manually scored using Intelligent Quantifier software (Millipore Corp., Bedford, Massachusetts).

2.2 Data analysis

Each sample was tested for departures from Hardy-Weinberg genotypic proportions with the exact test of Guo and Thompson (1992) using GENEPOP version 3.1 (Raymond and Rousset 1997); probability values were corrected with the sequential Bonferroni technique (Holm 1979; Rice 1989) with the initial significance level taken to be 0.05/number of loci (10). Similarly, testing of genetic homogeneity between samples was carried out as described by Raymond and Rousset (1995); this was accomplished with GENEPOP, and probability values were adjusted with the sequential Bonferroni technique with the initial significance level taken to be 0.05/number of loci (10).

F-statistics (Wright 1951) were computed according to Weir and Cockerham (1984) with GENETIX version 4.02, and the number of migrants exchanged per generation (N_em) was also estimated using GENETIX based on the approximation that $N_em = (1 - F_{st}) / 4F_{st}$ (Wright 1969); the significance of F_{st} values was tested by performing 500 permutations.

3. Results

We obtained data regarding genetic heterogeneity at 10 polymorphic microsatellite DNA loci from 141 deer representing four different locales. We calculated whether there were departures from Hardy-Weinberg for each locus within samples from each locality. Of the 40 comparisons possible, only one showed a statistically significant ($P < 0.005$) departure from Hardy-Weinberg, the *ILSTS65* locus at Reef Island. Tests of genetic homogeneity of samples showed that the 1999 and 2000 samples from Louise Island were not significantly different, nor were the 1998 and 1999 samples from SGang Gwaay, so these samples were pooled to increase sample size in further analysis. All locus-by-locus tests of allele frequency homogeneity between Moresby and Louise islands indicated that these two samples were not statistically different, and these were also pooled in further analysis; this pooled sample is referred to as "source."

Eight of the loci surveyed had two alleles, whereas two loci (*T32*, *ILSTS65*) had three alleles (Table 2). Two alleles were observed at locus *C89* in both the source population and Reef Island, whereas only a single allele was observed at this locus in the SGang Gwaay samples. Similarly, at locus *T273*, two alleles were found in the source population and on SGang Gwaay, whereas only a single allele was observed at this locus in the Reef Island samples. No alleles were absent in any of the other samples at any of the other loci. Locus-by-locus comparisons of allele frequencies between SGang Gwaay and the source population and between Reef Island and the source population indicate that these samples are not drawn from the same gene pool, suggesting population subdivision.

Further insight into the pattern of population subdivision between the locales sampled was gained by computing *F*-statistics (Table 3). There was a significant difference in genetic structure between SGang Gwaay and its source ($F_{st} = 0.1$, $P < 0.01$) and between Reef Island and the source ($F_{st} = 0.072$, $P < 0.01$). There were also significant differences between SGang Gwaay and Reef Island ($F_{st} = 0.079$, $P < 0.01$). The N_em values derived from these F_{st} values suggest that 2.23 migrants per generation are exchanged between SGang Gwaay and the source population, while 3.22 migrants are exchanged per generation between Reef Island and the source population.

4. Discussion

We have used microsatellite alleles to estimate deer colonization events for offshore islands of Haida Gwaii. Our data are inconsistent with a single colonization event but rather suggest high levels of dispersal, approximately 2–3 deer per generation among the islands. As generation time in black-tailed deer on Haida Gwaii is 2 or 3 years, this suggests a persistent dispersal of about one deer per year to both Reef Island and SGang Gwaay. As Reef Island represents one of the most remote islands in the archipelago, there will probably be even higher migration rates among the more numerous, more proximate islands in the archipelago.

It is possible that our results may have overestimated migration rates among the islands. This is because the method used to calculate migration does not

Table 2
Allele frequencies for all microsatellite loci in Sitka black-tailed deer samples from Haida Gwaii

Locus	Allele	Source	SGang Gwaay	Reef
DeerT7	1	0.24	0.316	0.07
	2	0.76	0.684	0.93
	N[a]	50	38	50
ILSTS65	1	0.212	0.132	0.108
	2	0.692	0.513	0.608
	3	0.096	0.355	0.284
	N	52	38	51
DeerC89	1	0.279	0	0.13
	2	0.721	1	0.87
	N	52	38	50
DeerT273	1	0.167	0.027	0
	2	0.833	0.973	1
	N	51	37	51
OarJMP1	1	0.288	0.486	0.45
	2	0.712	0.514	0.55
	N	51	37	50
LSTS001	1	0.5	0.139	0.255
	2	0.5	0.861	0.745
	N	51	36	49
DeerT32	1	0.038	0.081	0.19
	2	0.798	0.446	0.61
	3	0.163	0.473	0.2
	N	52	37	50
T193	1	0.346	0.197	0.48
	2	0.654	0.803	0.52
	N	52	38	49
ILSTS52	1	0.298	0.368	0.373
	2	0.702	0.632	0.627
	N	52	38	51
Cervid 1	1	0.817	0.855	0.51
	2	0.183	0.145	0.49
	N	52	28	51

[a] *N* = number of animals successfully analyzed for each locus.

Table 3
Pairwise F_{st} and N_em between Sitka black-tailed deer source populations from Moresby/Louise islands and offshore islands (Reef and SGang Gwaay) on Haida Gwaii

	F_{st}[a]	
	SGang Gwaay	Reef
Source (Moresby/Louise islands)	0.1	0.072
SGang Gwaay		0.079
	N_em	
	SGang Gwaay	Reef
Source (Moresby/Louise islands)	2.23	3.22
SGang Gwaay		2.92

[a] All F_{st} values are significant ($P < 0.01$).

distinguish between ongoing genetic exchange and historical association between locales. Similarity in allele frequencies can result from a single recent colonization event, with only a small amount of divergence due to genetic drift. Currently, we cannot exclude this possibility, but suspect that it is unlikely. At SGang Gwaay, where we estimate about two migrants per generation or one per year based on genetic data, direct empirical observations by a Haida resident on the island (Captain Gold, pers. commun.) show 10 individual dispersal events over a 30-year period (1970–2000), or about 1 every 3 years. This count will be highly conservative, as the observational period represents only a small proportion of the total time. Consequently, the number of deer swimming to the islands will be substantially higher; as a result, our estimates of one per year are probably conservative rather than overestimated. The high estimated migration rate between SGang Gwaay and Reef Island (Table 3), which seems improbable given the geographical separation of these two islands, is probably due to ongoing gene flow from the common source population (Moresby/Louise islands), rather than actual direct exchange of genetic material through migration between SGang Gwaay and Reef Island.

Several conservation implications emerge from our genetic results. Firstly, deer dispersal events, even among the more distant of the offshore islands, appear to be common. If true, single-event deer removal programs will be ineffective as an ecological tool. A single new female colonist and a single male can potentially generate a population near carrying capacity within a decade on each of these islands. Consequently, these islands with deer removal would require yearly assessment for deer occurrence and removal. Secondly, while empirical estimates of the original colonization of individual islands by deer obtained by dendrochronological analyses (Vila and Martin this volume, and references therein) suggest that most islands were already heavily impacted around the mid-20th century, our genetic data on dispersal are consistent with an initial colonization shortly after the late-19th- and early-20th-century introduction on Graham and Moresby islands.

Acknowledgements

We are grateful to Captain Gold and Doug Burles for information on incidence of swimming deer in Gwaii Haanas. T.E. Reimchen acknowledges the Natural Sciences and Engineering Research Council of Canada for continued support (Grant A2354).

Literature cited

Carl, G.C.; Guiget, C.J. 1972. Alien animals in British Columbia. B.C. Provincial Museum Handbook 14, Victoria, B.C. 102 pp.

DeWoody, J.A.; Honeycutt, R.L.; Skow, L.C. 1995. Microsatellite markers in white-tailed deer. J. Hered. 86: 317–319.

Foster, J.B. 1965. The evolution of the mammals of the Queen Charlotte Islands, British Columbia. B.C. Provincial Museum Occasional Paper 14, Victoria, B.C. 130 pp.

Guo, S.W.; Thompson, E.A. 1992. Performing the exact test of Hardy-Weinberg proportions for multiple alleles. Biometrics 48: 361–372.

Holm, S. 1979. A simple sequential rejective multiple test procedure. Scand. J. Stat. 6: 65–70.

Jones, K.C.; Banks, J.D.; Levine, K.F. 2000. DNA-based genetic markers in black tailed and mule deer for forensic applications. Calif. Fish Game 86: 115–126.

Jones, K.C.; Levine, K.F.; Banks, J.D. 2002. Characterization of 11 polymorphic tetranucleotide microsatellites for forensic applications in California elk (*Cervus elaphus canadensis*). Mol. Ecol. Notes 2: 425–427.

Kemp, S.J.; Hishida, O.; Wambugu, J.; Rink, A.; Longeri, M.L.; Ma, R.Z.; Da, Y.; Lewin, H.A.; Barendse, W.; Teale, A.J. 1995. A panel of polymorphic bovine, ovine and caprine microsatellite markers. Anim. Genet. 26: 299–306.

Lumsden, J.M.; Lord, E.A.; Montgomery, G.W. 1996. Characterisation and linkage mapping of ten microsatellite markers derived from a sheep × hamster cell hybrid. Anim. Genet. 27: 203–206.

Nelson, R.J.; Beacham, T.D.; Small, M.P. 1998. Microsatellite analysis of the population structure of a Vancouver Island sockeye salmon (*Oncorhynchus nerka*) stock complex using nondenaturing gel electrophoresis. Mol. Mar. Biol. Biotechnol. 7: 312–319.

Raymond, M.; Rousset, F. 1995. An exact test for population differentiation. Evolution 49: 1280–1283.

Raymond, M.; Rousset, F. 1997. GENEPOP (version 3.1b): an updated version of GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. J. Hered. 86: 248–249.

Rice, W.R. 1989. Analyzing tables of statistical tests. Evolution 43: 223–225.

Sambrook, J.; Fritsch, E.F.; Maniatis, T. 1989. Molecular cloning: a laboratory manual. 2nd ed. Cold Spring Harbor Laboratory Press, New York.

Weir, B.S.; Cockerham, C.C. 1984. Estimating F-statistics for the analysis of population structure. Evolution 38: 1358–1370.

Wright, S. 1951. The genetical structure of populations. Ann. Eugenics 15: 323–354.

Wright, S. 1969. Evolution and genetics of populations. Vol. II. The theory of gene frequencies. University of Chicago Press, Chicago, Illinois.

Lessons from elsewhere

Caption: Getting across the fence to survey an experimental enclosure on Anticosti Island
Credit: RGIS, Jean-Louis Martin

Science and the management of introduced species

Daniel Simberloff

Abstract

We can manage introduced species in three ways. First, we can keep them out. Second, if they get in, we can discover them quickly and attempt to eradicate them. Third, if they establish widely and are determined to be harmful and ineradicable, we can maintain them at levels low enough that impacts are acceptable. The role of science in managing introduced species varies. Scientific research is often crucial to understanding the ecological impacts of an invader, and this understanding can spur actions to attempt to keep them out. On the other hand, detailed scientific research usually plays little role in attempting to discover introductions quickly and to eradicate them. Once an introduced species is widely established, some activities to manage it at acceptable levels, such as repeated weeding, require little science. Others, particularly in the realms of biological control and ecosystem management, may demand substantial pioneering research. In any event, a comprehensive, coordinated approach with clear, quantifiable goals is needed for a successful response to introduced species.

1. Introduction

The first option that should be considered in managing an introduced species is doing nothing (Simberloff 2002a). A minority of introduced species actually have serious ecological or economic impacts. The "tens rule" (Williamson and Brown 1986; Williamson 1996) has held up fairly well (cf. Lockwood et al. 2001): about 10% of established introduced species become pests. The problem is that the tens rule does not identify which 10% are likely to be problematic and therefore should be targeted for exclusion, eradication, or long-term maintenance management. Invasion biologists have not been very adept at predicting which species will be problems (Williamson 1996), although some recent progress has been made by focusing on particular taxa, such as pines (e.g., see Rejmánek and Richardson 1996). Additionally, some introduced species that have initially been enormous problems or appeared to be headed in that direction have subsequently declined to insignificance, sometimes with startling rapidity (Simberloff 2002a). On the other hand, sometimes there are lag times in the transition from harmless, recent immigrant with small population size to widespread horror (Crooks and Soulé 1996). The latter phenomenon has been more widely cited than the former, but neither has been subjected to much study. The fact that most introduced species do not become substantial invaders of native ecosystems or cause major economic problems presents a dilemma to policymakers and managers, as any management procedure entails costs, and resources are always limited. The temptation to do nothing is thus strong; doing nothing is probably, in fact, the most widely chosen option, precisely because it saves money in the short term. One key way in which science can aid management is to show which invaders are actually causing impacts, and, since some of these impacts are quite subtle, the research needed to identify them can be difficult and detailed.

Given our rather poor ability to predict impacts of invasions, it is only prudent to consider all introductions as potentially harmful and at least to examine proposals for deliberate introductions very comprehensively. Because so few harmful introductions seem to wane spontaneously, it would also not be prudent for a manager to bank on a problem disappearing without active management. There are three stages at which managers can minimize the impacts of introductions (Simberloff 2002a):

1. They can keep them out.
2. If they get in, they can be detected quickly and eradicated.
3. If they are not detected quickly and/or eradication fails, various techniques can be employed to maintain their populations at low densities.

2. Keeping them out

As in medicine, an ounce of prevention is worth a pound of cure—keeping out invaders is less costly than trying to reduce or eliminate them. Interdiction must be targeted at two categories of introductions—deliberate and inadvertent ones—that call for somewhat different procedures. It is depressing that, where data exist, deliberate introductions typically account for about half of all introductions and that detrimental effects arise from deliberately introduced species at least as frequently as from inadvertently introduced ones (e.g., see Gordon and Thomas 1997). In the Queen Charlotte Islands, of 10 extant introduced mammal species, 8 were deliberately introduced (5 by government agencies).

These include the five species that may have harmful impacts on native ecosystems (Golumbia 2000; Engelstoft and Bland 2002): raccoon *Procyon lotor*, black-tailed deer *Odocoileus hemionus*, muskrat *Ondatra zibethica*, beaver *Castor canadensis*, and American red squirrel *Tamiasciurus hudsonicus*. Much less is known about the means by which plants were introduced to the Queen Charlotte Islands (Engelstoft and Bland 2002), but it is remarkable that Scotch broom *Cytisus scoparius*, considered in many other regions to be a major threat to entire ecosystems (Bossard 2000; Hendrickson 2002), was deliberately brought to the Queen Charlotte Islands by a private citizen (Engelstoft and Bland 2002), and that both Scotch broom and gorse *Ulex europaeus*, another extremely harmful invader in other regions (Hoshovsky 2002), have apparently been used locally for landscaping (T. Golumbia, pers. commun.).

The fact that many introduced species are deliberately introduced suggests that keeping out many invaders should be straightforward—simply decide which planned introductions carry substantial risk of being problematic and forbid them. In most parts of the world, this effort has not been very successful, for several reasons. First, there is often dispute about whether an introduction is likely to be harmful or whether the harm is likely to outweigh the benefit. Different stakeholders have different perceptions. Black-tailed deer in the Queen Charlotte Islands are seen as a boon by hunters and a bane by plant gatherers (Engelstoft 2002a).

Second, impacts of introduced species are notoriously hard to predict (Williamson 1996), although a well-established principle is that species problematic in one place have a high probability of being problematic when introduced to others (Lonsdale 1999). This unpredictability means that formal quantitative risk assessment procedures for introduced species are at a very early stage of development and cannot generally yield accurate probabilities and cost estimates (Simberloff and Alexander 1998). Nevertheless, the rapid expansion of global trade and the associated multilateral trade treaties such as those of the World Trade Organization have led to a situation in which introductions are assumed "innocent until proven guilty," and "proof of guilt" must be established by formal risk assessment procedures (U.S. National Research Council 2000; Simberloff 2001). The upshot is that, at the international level, it is difficult for a nation to exclude a specific introduced species or a product that might carry one without being charged with and convicted of economic protectionism. The recent rejection by the World Trade Organization of Australia's attempt to exclude frozen imported salmon from Canada is partly due to the Australians' inability to provide a quantitative assessment of the risk that the salmon would carry disease organisms that might harm native fishes (Victor 2000). This rejection is in spite of the fact that whirling disease, which arrived in frozen trout from Sweden, has already devastated many North American rainbow trout fisheries (Markiw 1992; Nickum 1999).

The fact that the Queen Charlotte Islands are islands wholly within Canada and have a small population to some extent simplifies and facilitates the possibility of exclusion. International trade will not specifically target the Queen Charlotte Islands, and their insularity lessens (but does not preclude) the likelihood that an invader in mainland Canada will get to the archipelago. However, effective exclusion would require the populace as a whole to accept the need for regulation, no matter how innocuous or beneficial an individual citizen may deem a potential introduction, and the establishment of both enforceable regulatory procedures and an interdiction apparatus to enforce them. In particular, there must be the acceptance of the principle that every potential introduction is seen as guilty until proven innocent and subject to expert scrutiny before it can be imported (Simberloff 2000). Even nations such as Canada and the United States, in which there is substantial awareness of the risk of damage from introduced species, have not adopted this principle. New Zealand's 1993 *Biosecurity Act* enshrines this notion and has been crucial to the substantial success achieved by that nation in curbing harmful introductions (New Zealand Parliamentary Commissioner for the Environment 2000).

Inadvertent introductions are difficult to preclude; these are species that hitchhike on products (such as insects in fruit or plant material) or exploit pathways that might carry many invaders, such as ballast water or untreated wooden packing. For large ports with much shipping and passenger activity, interdiction of such invaders is a laborious process, although sufficient effort can be very effective (New Zealand Parliamentary Commissioner for the Environment 2000; Baskin 2002). However, once again the insularity and low population of the Queen Charlotte Islands can help. Although the major effort at closing down pathways will have to be a national effort by the Canadian government, special procedures can be used to keep inadvertent introductions from getting from the rest of Canada to the archipelago. Ecuador, for example, instituted a special law in 2000 for the Galápagos archipelago, which is under siege from invaders because of increased tourism and attendant development (Baskin 2002). Some species and products are prohibited or restricted in the Galápagos, including live animals, many plants, and some foodstuffs. Movement among the different islands is also regulated. A government agency is charged specifically with interdiction and includes 36 inspectors present at all ports of exit and entry. Some inspection takes place on the mainland, in Quito and Guayaquil, and a special dock and treatment facility are planned in Guayaquil for produce and other items destined for the islands. Thorough inspection in the Queen Charlotte Islands could largely shut down certain pathways for potentially damaging introductions. For example, road ballast and other landscaping materials could be carefully inspected for seeds of Scotch broom, gorse, various thistles, and other weeds (cf. Prasad 2001). Visual inspection and germination procedures are two possible techniques.

3. Eradication

Many people believe that eradication of invaders is a difficult, expensive proposition with low probability of success, particularly if a species is widely established. However, there have been many successful eradications, not only from islands but from continental regions, and not simply of very recent invaders (Simberloff 2002b). Unfortunately, many good eradication projects have not been

well publicized, and there is no real "science" of eradication, with a journal primarily devoted to eradication efforts and a hierarchical literature helping researchers learn from past efforts. Although smallpox has been eradicated from the entire Earth (except for vials in Atlanta, Moscow, and perhaps a few terrorist redoubts) (Fenner et al. 1988), and *Anopheles gambiae*, the African mosquito vector of malaria, was eradicated from 31 000 km^2 of northeastern Brazil (Davis and Garcia 1989), a disproportionate fraction of recent eradications have been of mammals from islands (e.g., Veitch and Bell 1990; Chapuis and Barnaud 1995; Day and Daltry 1996a,b; Pascal 1996; Day et al. 1998; Pascal et al. 1998; Varnham et al. 1998; Bell 1999; Tershy et al. 2002). The eradication of Norway rats *Rattus norvegicus* from Langara Island (Kaiser et al. 1997; Taylor et al. 2000) is one of the most striking successes. This is the largest island (3105 ha) from which rats have been eradicated, although other large islands have also been cleared recently of rats (e.g., 1965-ha Kapiti Island, New Zealand [New Zealand Department of Conservation 2002], and 800-ha Saint-Paul Island [Micol and Jouventin 2002]). It is worth noting that although eradication of plants is often claimed to be much more difficult than that of animals (e.g., Rejmánek and Pitcairn 2002), some plant populations have been eradicated. Two noteworthy projects rapidly approaching successful conclusion are the campaign to eradicate kochia *Kochia scoparia* from 3200 ha spread out over 900 km in Western Australia (Randall 2001) and the project to rid Laysan Island of the sandbur *Cenchrus echinatus* (Flint and Rehkemper 2002).

A closer look at which eradication projects have succeeded and which have failed (Myers et al. 2000; Simberloff 2002b) suggests several features that typify successes:

a) *A can-do attitude*: In almost every instance, from the global eradication of smallpox down to the elimination of rats from small islands, someone had to be willing to make a wholehearted effort to eradicate, in spite of naysayers claiming it was impossible. My favourite example is a private group of scientists and citizens (the Island Conservation and Ecology Group) that has managed, on a shoestring budget, to eradicate various combinations of feral cats *Felis catus*, Norway and black rats *Rattus rattus*, house mice *Mus musculus*, rabbits *Oryctolagus cuniculus*, goats *Capra hircus*, sheep *Ovis aries*, and burros *Equus asinus* from several islands in northwest Mexico (Tershy et al. 2002). The New Zealanders have become world leaders in vertebrate eradication (e.g., see Veitch and Bell 1990; Veitch and Clout 2002), partly by virtue of a relentless optimism that if they worked hard enough, they could do it.

b) *Sufficient economic resources to complete the project:* Although enthusiasm and efficiency can compensate for low funding, particularly in situations in which a species has recently invaded or the target area is small and well delimited, such as a small island or a lake, many eradication projects are carried out over large areas and require correspondingly large budgets (Myers et al. 2000; Simberloff 2002a,b). Usually the benefit of eradication over maintenance management is that eradication obviates the need for continuing control expenses; the initial investment must then be large enough to see the project through to completion. Public agencies have sometimes moved to reduce funding for a project when it is so near to completion that the invader has ceased to be a problem (Simberloff 2002b). Depending on the exact costs of the eradication attempt and alternative maintenance management procedures and on the degree and persistence of control achieved by an incomplete eradication campaign, limiting funding before complete eradication can be economically foolish.

c) *Clear lines of authority, and enforcement powers:* Because individuals can subvert an eradication campaign (e.g., by importing and/or releasing individuals of the target species), because some eradications must be undertaken on private property, and because some target areas fall under several governmental jurisdictions, it is important that someone or some entity be clearly in charge and be able to compel cooperation (Myers et al. 2000; Simberloff 2002b). In some cases, killing large, charismatic vertebrates has generated vocal opposition, either from animal rights organizations or from hunters (references in Simberloff 2002b). Most eradication campaigns for conservation or environmental purposes (rather than agriculture or human health) have been on isolated islands with few or no inhabitants (e.g., the small New Zealand islands). So enforcement has not been a big problem. For eradications on the mainland, there has always been a promised economic or health benefit to at least some stakeholders, and this fact has helped to get the public behind them; often a few dissenters remain, however, and someone has to be able to force people to cooperate.

d) *Appropriate biology of the target organism:* Although sufficient effort can probably eliminate any species over a small area, some species are easier to eradicate than others. The feasibility of eradicating some widespread invaders requires their having appropriate biology. Some traits conducive to eradication are obvious (Simberloff 2002a): mammals, especially large ones, are easier to eradicate than insects, while plants with a soil seed bank are less tractable than those without one. Other important features are less apparent. For example, the fact that smallpox has no nonhuman or long-term carriers was crucial (Fenner et al. 1988), as was the fact that *Anopheles gambiae* in Brazil was found almost wholly near buildings (Davis and Garcia 1989).

Several features often assumed to be necessary for the success of an eradication effort are not, in fact, automatic prerequisites:

a) *Exhaustive scientific knowledge of the target species:* It is often assumed that detailed knowledge of the biology of the target species is required to control it. In fact, it is commonplace among invasion biologists that appeals for increases in research budgets are

justified on the grounds that they will lead to much better control. However, many eradication projects have succeeded with minimal background biological research (Simberloff 2003). As one dramatic example, the Caribbean black-striped mussel *Mytilopsis sallei* appeared in Darwin Harbor in 1999 and was discovered within 6 months, before it had spread outside 12.5-ha Cullen Bay (Bax et al. 2002). Within 9 days, the Australian government had quarantined the entire bay and treated it with 187 tonnes of liquid bleach and 7.5 tonnes of copper sulfate, thereby eradicating this mollusc (as well as killing all other living organisms in the bay). There was little empirical research on concentrations of these poisons or on exotic chemicals that might have been employed. Because no species were restricted to the bay and many had planktonic larvae, there was reason to believe that recovery of the native biota would be rapid, and this has proved to be the case.

This scorched earth approach has been applied successfully to other invaders. For instance, the white-spotted tussock moth *Orgyia thyellina* appeared in a suburb of Auckland, New Zealand, in about 1996, and the government launched an eradication campaign the next year, before it had spread. They sprayed with *Bacillus thuringiensis*, having ascertained that the moth is susceptible to this bacterium. They did not conduct empirical research on the possible impact of the spray on other lepidopterans, despite the fact that *B. thuringiensis* can kill many other lepidopterans, and similar campaigns have aroused concern about nontarget victims (Miller 1990; Sample et al. 1992). There is no organized monitoring to study this impact. Nor was there detailed study of the possible impact of the tussock moth on native plants, although there was every reason to believe it could have been substantial. Rather, the government acted quickly with overwhelming force (New Zealand Ministry of Agriculture and Forestry 1998; Anon. 1999; Clearwater 2002).

There is occasionally an appeal to conduct massive eradication campaigns as experiments, with a range of treatments and controls, in the spirit of adaptive management (which is discussed below). For example, this very issue arose in the campaign to eradicate the invasive tropical alga *Caulerpa taxifolia* from two California sites (cf. Meinesz 2001), with scientists seeking tests of various concentrations of the bleach used as an algicide and the state coordinating agency demanding (and using) massive amounts at the outset, on the grounds that the priority is to eradicate the infestations before they spread, a goal that could be compromised by controls and low-concentration treatments. If an invasive species is already so well established that local increase is not an issue and if it is unlikely to spread to other sites (as might be the case, for example, for a terrestrial vertebrate on one island in an archipelago), an adaptive management approach to eradication might be warranted. However, if an eradication is aimed to control a recent invader before it prospers and disperses more widely, a nonexperimental, brute force method is surely justified if it carries a substantial probability of success.

Even well-established invaders can sometimes be eradicated with little or no scientific research. The Island Conservation and Ecology Group mentioned above has used trapping and hunting to achieve remarkable eradications (Tershy et al. 2002; Wood et al. 2002). This is not to say that great knowledge and experience were not brought to bear in this project; determining optimal design and placement of traps, for example, takes great skill, but it is perhaps more in the realm of art than science. The Australian project to eradicate kochia was mounted after the weed had already infested 3200 ha, but it is rapidly approaching success (5 ha at last count) and entailed simply heavy use of a variety of herbicides, not population biological research (Randall 2001; R. Randall, pers. commun.). I do not mean to imply that any eradication program can aspire to success without much scientific research. For example, various insect eradications using the sterile male technique have been greatly facilitated by detailed population study and modelling (references in Simberloff 2003). Rather, my point is that some eradications can be accomplished without elaborate methods, and, particularly in the early stages of an invasion, the crude application of brute force might be worth trying to forestall the necessity of long-term management.

b) *Early detection:* It is true that eradication is much easier and cheaper before a new invader has spread from its initial beachhead. Some successful eradications of widespread invaders have cost millions of dollars (Simberloff 2002b). This fact has generated much interest in the development of early warning/rapid response systems (e.g., Westbrooks et al. 2000; Timmins and Braithwaite 2002). Other than improved interdiction procedures, probably no single development could aid the war against introduced species as much as improved early warning and rapid response capability. However, early detection is not a *sine qua non* of eradication; with determination and skill, even longstanding invasions can sometimes be eradicated.

c) *Low probability of rapid reinvasion:* One reason a large fraction of eradication efforts have been undertaken on islands is that islands are isolated, lessening the likelihood of quick reinvasion. Certainly it is less desirable to attempt eradication if there is a high probability that the same species will simply reinvade quickly even if the eradication succeeds. In some circumstances, however, it might be worth attempting eradication anyway (Simberloff 2002a,b). For instance, trade regulations may prohibit importation of a product unless the region of origin can be certified as free of some invasive pest. If eradication can be achieved in such a case, but only temporarily, it may be economically beneficial nevertheless to eradicate the pest repeatedly. This is exactly the situation with the Asian race of the gypsy moth *Lymantria dispar* in British Columbia (Myers et al. 2000; Nealis 2002;

Simberloff 2002a), where 20 campaigns to eradicate the moth with *Bacillus thuringiensis* have apparently succeeded, only to be followed by reinvasion. The effort, although costly (the largest of these eradications cost $6.5 million), is justifiable on the grounds that the potential economic damage from establishment of the moth would be staggering, not least because products from the region could be prohibited or subjected to expensive quarantine or treatment procedures. As another example of a circumstance in which attempted eradication might be the best option even in the face of reinvasion, the expected cost of an eradication might be low, the benefit of even temporary absence of the pest great, and expected time to reinvasion not too short.

Finally, it is important to observe that eradication does not by itself constitute restoration (Towns et al. 1997; Zavaleta et al. 2001; Simberloff 2002b). Various unforeseen consequences may ensue. For example, elimination of a herbivore may lead to an unexpected increase in an introduced weed (e.g., see Dash and Gliessman 1994), while elimination of a predator may lead to increased densities of one or more prey species. Eradication (or maintenance management) of one introduced species may simply lead to the proliferation of another. Thus, it is important to think carefully about what the actual desired goal of an eradication is, beyond simply removing a nonnative element from the community, and also to be prepared to respond nimbly to unexpected developments in the wake of an eradication. Here is an important locus of research, as the direct and indirect interactions between species are sometimes recondite and often can be elucidated—and perhaps predicted—only after intensive scientific study.

4. Maintenance management

If eradication of a problematic invader fails or is not attempted, there are four main approaches to maintaining low populations of a species to minimize its impact: mechanical control, chemical control, biological control, and ecosystem management (Simberloff 2000, 2002a). In some instances, two or more of these methods can be used together. Although none is a silver bullet, each has been effective in particular cases.

4.1 Mechanical control

Mechanical control encompasses many techniques, such as hand-pulling plants and shooting or trapping animals. Although complex machinery can be used, such as various gadgets to remove invasive plants, mechanical control often involves very simple methods but massive amounts of labour. Organized volunteer labour can be remarkably effective. For instance, the State Nature Preserves Commission of the State of Kentucky has had good success controlling musk thistle *Carduus nutans* by using volunteers convicted of drunk driving to pull it up (J. Bender, pers. commun.). An important point here is that initial decline in thistle density was low; this was doubtless because musk thistle seeds may persist in the soil for at least 10 years (Desrochers et al. 1988; Beck 1999). However, within a few years, density had declined greatly, and it has remained low. Thus, persistence was crucial to the success of this project, plus the continuous availability of a substantial pool of drunk drivers. Of course, paid labour is also an option for such efforts.

Well-publicized volunteer labour has an added advantage—it sensitizes and educates the public to the general problem of introduced species. For example, in Victoria, British Columbia, the centrepiece of the Garry Oak Meadow Invasive Plant Removal Project is repeated "broom bashes" to remove Scotch broom (Econews 1998). These generate much publicity about Scotch broom and other introduced plants (e.g., Curtis 1996) and engage young people such as elementary school students and Girl Guides in the battle against introduced species (V.G. Nealis, pers. commun.).

Because Scotch broom introduced elsewhere has a persistent soil seed bank and has been a major fire hazard, it will require persistent control, and most effective methods are mechanical (Bossard 2000 and pers. commun.). This species often remains at low density until fire, logging, grazing, soil movement, or some other disturbance causes many dormant seeds to germinate, leading to rapid spread (e.g., Bossard 1991; Prasad 2001). In some areas, prescribed burns in combination with other methods have been effective, but this approach presents the danger of a wildfire. Broom can be removed with a brushcutter cutting close to the ground, but resprouting is a problem, and the method has to be applied repeatedly because of the soil seed bank. In Golden Gate National Park, California, Scotch broom has been well controlled by teams of volunteers with root wrenches. However, for all these methods, the fact that Scotch broom seeds remain viable in the soil for up to 10 years means that the effort will have to be sustained. Chemical approaches to broom control will be discussed below.

Gorse *Ulex europaeus* is present in the Queen Charlotte Islands and presents similar threats and management problems to those of Scotch broom—it may spread slowly, and largely in the wake of disturbances, but once well established, it is a fire hazard and difficult to control, partly because of its soil seed bank (Hoshovsky 2002). It even destroyed the town of Bandon, Oregon, by a wildfire spawned in gorse patches that surrounded and pervaded the town (Holbrook 1943). Although a variety of methods have been employed to manage gorse, most success has been with mechanical methods, often combined with chemicals (Hoshovsky 2002). Fire has been used successfully to control gorse thickets, but this effort must also be long term because of the soil seed bank and the fact that fire may induce gorse germination. It is small wonder that two attempts to eradicate gorse infestations in the Queen Charlotte Islands by single burns were unsuccessful (Engelstoft and Bland 2002).

Hunting and trapping can be remarkably effective controls against some animals, if pursued at high enough levels and with unwavering consistency. The Alberta Rat Patrol, which has kept Alberta largely free of Norway rats at a government cost of approximately $350 000 per year, is a notable example of how willingness to attempt what might at first seem a quixotic quest has led to stable, long-term

control of a major pest at very low levels (Bourne 2000; Holubitsky 2000). First discovered at the eastern border of Alberta in 1950, rats are primarily controlled in the province by rigorous inspection in a 29 × 600 km border zone, with food source elimination, anticoagulant baits, and hunting by seven provincial rat patrol officers playing key roles. The population has been reduced to a point where every year about 100 infestations are discovered and destroyed, and discovery of a single rat in Calgary or Edmonton is a major news story.

However, hunting by itself is rarely an effective control measure for animals with a sufficiently high reproductive rate. For instance, wild boar, feral pigs *Sus scrofa*, and their hybrids are extremely difficult to control this way. A continuous removal rate of at least 70% is needed (Dzieçiolowski et al. 1992; Caley 1993), and even a short relaxation can lead to a very rapid increase. Thus, if control is a real goal, rather than maintaining a population for sport hunting, various other techniques must be employed: fencing, trapping, hunting (especially with dogs), snaring, and poisoning (Coblentz and Baber 1987; Hone and Stone 1989; Katahira et al. 1993; Kessler 2002; Schuyler et al. 2002).

The varied and primarily harmful impacts of deer, including Sitka black-tailed deer, on forests and their denizens are widely documented worldwide (e.g., see Gill 1992a,b; Bergström and Bergqvist 1997; Fuller and Gill 2001; Gill and Beardall 2001; Kirby 2001; Rooney 2001), and similar impacts are now being demonstrated in the Queen Charlotte Islands (e.g., see Pojar and Banner 1984; Daufresne and Martin 1997; Baltzinger and Martin 1998; Golumbia 2000; Engelstoft and Bland 2002; Martin and Baltzinger 2002; Vila et al. 2003). On the other hand, Sitka black-tailed deer are favoured by many in the archipelago for sport and subsistence hunting (Engelstoft 2002a; Engelstoft and Bland 2002). This lack of consensus makes it unsurprising that there is no overall plan for managing deer; a desired outcome must be clearly articulated before one can plan.

Golumbia (2000) feels that eradicating deer on Haida Gwaii (Queen Charlotte Islands, British Columbia) is neither feasible nor socially desirable. I will not address social or environmental desirability, but I suspect that eradicating deer on Haida Gwaii or any of the other islands is technically feasible, given sufficient determination to do it (see section 3 above) and the wealth of successful mammal eradication programs on islands, even large ones (e.g., see Veitch and Clout 2002). It is also unclear that simply reducing deer densities in a controlled way (as is currently being done experimentally on two of the smaller islands in the Queen Charlotte archipelago; Golumbia 2000) will stem environmental damage sufficiently, unless the control is monitored and maintained very carefully. Deer can reduce biodiversity at less than 25% of their carrying capacity (deCalesta and Stout 1997). Martin and Baltzinger (2002) have recently shown that western redcedar *Thuja plicata*, which is drastically reduced by Sitka black-tailed deer, regenerates better in areas in which deer are hunted for sport. Historically, however, reliance on private hunters to control deer has led to problems sustaining consistent pressures (Diefenbach and Palmer 1997; Fraser 2000; Nugent et al. 2001; Rooney 2001), and, as with boar and pigs, even a short respite can allow deer to increase their populations quickly. The ultimate goal on these two islands is eradication (J.-L. Martin, pers. commun.). The potentially rapid reproductive rate of deer means that final success will be greatly delayed if the current reduction to 5% or less of the original population is used to justify relaxing the effort. As noted in the discussion of eradication above, limiting funding as numbers of a target pest dwindle can stymie a project and lead to great unnecessary expense.

Deer are strong swimmers, and any management program (including eradication as well as maintenance management) would have to include an assessment of recruitment or reinvasion probability. Chemical baits combined with hunting have proven effective in some deer management programs, and the technology is sufficiently developed that nontarget impacts can be minimized (Nugent et al. 2001; G. Nugent, pers. commun.).

4.2 Chemical control

Many of the above examples of successful eradication entail the use of herbicides, rodenticides, insecticides, and other chemicals (including microbial pesticides). Chemicals also have a potential role as maintenance management tools, alone or in combination with mechanical control and ecosystem management.

The well-known human health and other nontarget impacts of early-generation pesticides, such as DDT and other chlorinated hydrocarbons, are legendary (cf. Carson 1962) and have led to a type of chemophobia among many environmental advocates (Williams 1997). The blanket opposition of the Council of the Haida Nation to the use of herbicides to control invasive plants on Haida Gwaii (Engelstoft 2002b), rather than advocating judicious, case-by-case consideration, seems to exemplify such chemophobia. Many modern pesticides, however, have far fewer (if any) nontarget impacts and, if used judiciously, can be useful in managing invaders. For instance, a chemical mixture applied directly to individual cut plants has effectively controlled Scotch broom (Bossard 2000), but it is expensive and time-consuming, and the remaining dead biomass constitutes a fire hazard. Triclopyr ester (Garlon®) applied in low concentrations to basal bark is also effective and far cheaper, although the problem of dead biomass remains.

Many animals have been successfully controlled partly or wholly by chemicals. For instance, as discussed above in connection with the Alberta Rat Patrol, anti-coagulant baits are an integral part of the program. With attractive poison baits used for animal maintenance management (or eradication), it is important to arrange baits to minimize access of nontarget species. Scavengers are especially at risk of poisoning by baits or poisoned carcasses. For example, in the eradication of rats from Langara Island, Common Raven *Corvus corax* populations may have been at least temporarily depressed from mortality associated with scavenging baits and carcasses, and there may have been a lesser but similar effect on Bald Eagles *Haliaeetus leucocephalus* (Howald et al. 1999). In general, various techniques have been successfully employed to minimize

such nontarget impacts (e.g., Veitch 2002), but the problem is more severe for poisons used in an ongoing maintenance management program than in an eradication attempt.

Chemicals have two frequent disadvantages as parts of maintenance management compared with eradication programs. First, they are often expensive, particularly if used over large areas, as in many instances of management for environmental purposes. Second, species evolve resistance to pesticides, so that increasing amounts are required, and eventually the pesticide is ineffective against its target.

4.3 Biological control

Biological control seeks to establish a stable, homeostatic relationship, at low population densities, between an introduced pest and a natural enemy, which is deliberately introduced for this purpose (Greathead 1995). In agriculture and silviculture, some striking successes have been recorded by biological control (examples in Simberloff 2002a). These successes have led some managers to advocate biological control as a "green" alternative to chemical control; indeed, McFadyen (1998: 369) writes that "biocontrol offers the only safe, economical, and environmentally sustainable solution" to introduced weeds.

However, aside from the fact that many successful weed control projects (such as that for musk thistle described above) did not rely on biological control, several problems may arise with this technology (Simberloff 2002a). First, most biological control projects do not work. For instance, longstanding efforts to find effective biological controls for gorse (Hoshovsky 2002) and Scotch broom (Prasad 2001) have failed. On average, half or fewer of biological control introductions survive, and only a third of these survivors exert control on the target pest (Williamson 1996). Second, just as with some pesticides, some biological control agents have nontarget impacts (Simberloff and Stiling 1996). For example, the weevil *Rhinocyllus conicus*, introduced by the Canadian government to control musk thistle, now threatens several native thistle species in the United States (Louda et al. 1997; U.S. Department of the Interior 1997). There is much current controversy about the extent of nontarget problems (cf. Follett and Duan 2000). However, there is widespread, but not universal, agreement that to avoid this problem, only species highly adapted to a single target species should be used as biological control agents. Third, biological control agents can disperse much more easily than chemicals from areas of introduction to other regions in which they may cause harm. The dispersal of *Rhinocyllus conicus*, both on its own and by government agencies and private citizens in both Canada and the United States, is a good example. Fourth, biological control introductions are usually irreversible, as typical biological control agents (e.g., small insects) are among the most difficult species to eradicate. With chemical control, if the method does not work or has unexpected side effects, one can simply stop using it. With biological control, if the initial introduction has established a population, active means are required to remove it, and the probability of success is not high.

4.4 Ecosystem management

It is sometimes possible to manage an entire ecosystem so as to favour native species as a group over most invaders. For example, good pasture management keeps musk thistle from becoming a major weed, as it is outcompeted by native grasses (Louda 2000). Similarly, maintenance of a natural fire regime in the fire disclimax forests of the southeastern United States may have stemmed the invasion of introduced species (Simberloff 2001). Resource management agencies have lately become great enthusiasts of ecosystem management, although its potential role in managing introduced species is infrequently discussed. However, ecosystem management has been more a theoretical concept than a set of management techniques, and it has rarely been tested rigorously for an extended period; this problem is exacerbated by its frequent association with adaptive management (Simberloff 1998).

Thus, there are many technologies for maintenance management, and for each there are successes and also failures. No one technique is best for managing all introductions, but each has a role to play in particular projects, depending on the target pest, the setting, and experience in similar situations.

5. Discussion

The various approaches discussed above are, for the most part, targeted at single species. Eradication is, by its nature, about single species, and so are the various maintenance management procedures, except for ecosystem management. Some exclusion and interdiction activities are, of course, more broadly aimed, but the laws and regulations for allowing deliberate introductions are almost wholly in terms of the predicted impact of a single species whose introduction is sought. Further, both eradication and maintenance management procedures are essentially reactive. Although in many instances these various single-species reactive approaches have successfully dealt with particular invasions, and disallowing or interdiction of deliberate or unplanned introductions has sometimes forestalled what might have been harmful introductions, the entire approach is inefficient and simply not up to the task of dealing with an increasing flood of invaders (Schmitz and Simberloff 1997). This piecemeal and primarily reactive approach is insufficient for two main reasons:

a) Introduced species may interact to exacerbate one another's impacts, and the ways in which they interact are often quite unpredictable (Simberloff and Von Holle 1999). Introduced animals may feed on introduced plants and, at the same time, disperse their seeds, for example. In the Queen Charlotte Islands, a possible example of such "invasional meltdown" is that browsing by deer may increase squirrel predation on songbird nests (Martin et al. 2001; J.-L. Martin, pers. commun.). The deer cause an increase in Sitka spruce *Picea sitchensis*, and abundance of spruce, their main food in the archipelago, controls squirrel abundance. Squirrel abundance was shown to correlate with rates of nest predation. Both the deer and the squirrel were

introduced by government agencies (Engelstoft and Bland 2002), and I doubt that consideration was given in either case to the possibility that one of these species might affect the impact of the other.

b) It is inefficient and sometimes leads to incompatible management practices. So long as each species is dealt with individually, procedures that might simultaneously minimize impacts of several are unlikely to be considered. The idea of ecosystem management is, in essence, a plea to achieve more comprehensive, efficient control by managing many species at once. One reason it has not been employed more widely is that it runs counter to the predominant mode of dealing with introduced species. Absence of some overall guidance and plan can even lead to expensive, yet incompatible, methods being used by different agencies or people on the same pest, dooming the entire enterprise to failure. For instance, the Oregon Department of Agriculture, having failed to achieve adequate control of Scotch broom with backhoes, root wrenches, and herbicides, had found a promising biological control agent, the European beetle *Bruchidius villosus*. In 1999, they reared enough individuals for a field test, but a road crew of the federal Bureau of Land Management, in their Scotch broom control program, ripped out an entire patch of the plant with 250 newly released beetles (Barnard 1999). Finally, the very fact that we rely so heavily on eradication and maintenance management, rather than preclusion, is inefficient. As stated at the outset, an ounce of prevention is worth a pound of cure.

These considerations led Schmitz and Simberloff (1997) to suggest the need for a comprehensive management plan, centrally coordinated. In the United States, President Bill Clinton recognized this need for a comprehensive strategy and codified this recognition in his Executive Order 13112 of 3 February 1999. Interestingly, the Queen Charlotte Islands, with its draft strategic plan (Engelstoft 2002b), is as advanced in this regard as the United States. The U.S. National Invasive Species Council established by the Executive Order was mandated to establish a management plan for dealing with invasive species in the United States, and this plan was finally published in 2001 (U.S. National Invasive Species Council 2001).

The draft strategic plan for the Queen Charlotte Islands (Engelstoft 2002b) contains many laudable features and captures some of the best thinking of invasion biologists and managers. In its efforts to arrive at an overall estimate of the scope of the problem and to envision a coordinated response, it is in some ways ahead of the U.S. plan. Nevertheless, I feel two aspects of it are questionable and at least need clarification.

The plan stresses research, not only on life histories and demographic modelling of the various introduced species, but on genetic diversity and evolutionary change. The plan adopts the recommendations of Sakai et al. (2001), which basically justify the entire gamut of invasion biology research on the grounds that it will greatly aid management. Of course, increased knowledge of invasions in general and of specific invaders in particular cannot hurt management, and in some areas it is a prerequisite. For instance, it is crucial to understanding the impacts, even the subtle ones, of well-established invaders. The efforts of the Research Group on Introduced Species are an excellent local example of such research. However, as I have indicated above, many aspects of successful management need little or no research. This is especially true for quick attempts to eradicate recent invasions through the use of brute force, but there are also some effective long-term maintenance management procedures that do not rest on extensive scientific research (although, of course, they are, in a sense, experiments in their own right, since we do not know if they work until they are tried for an extended period). Of course, much research has already been conducted elsewhere on many current and potential invaders of the Queen Charlotte Islands, and the literature on this research will be a valuable tool, but there is a limit to the amount of *in situ* research that can be funded and that is truly required. In the worst case, the need for additional research can even be invoked as a reason for inaction (Simberloff 2003). On the other hand, political and economic considerations can be invoked to attempt to reduce research that is truly important for management. It is crucial for both policymakers and scientists to be judicious and far-sighted in determining what research should be advanced for management purposes.

Finally, the plan has a distressing tendency to use fuzzy terms that are not easily made operational, such as ecosystem health and ecosystem integrity (cf. Simberloff 1998). The goal of restoration in the plan, is not approximation of some previous state, but rather a state of ecological integrity. Ecological integrity was at one time defined (Society for Ecological Restoration International 2002) as "a critical range of variability in biodiversity, ecological processes and structures, regional and historical context, and sustainable cultural practices," although this part of the Society web site no longer exists. How much variability? Which ecological processes and structures? What exactly is meant by "sustainable"? It is important for restoration in general, and management of introduced species as part of it, to have clearly defined, quantitative goals, and the set of terms that dominates the plan will not easily lead to such goals. It is hard to imagine the plan being made operational in these terms. There are even inherent contradictions. Ecological restoration is defined (Society for Ecological Restoration International Science and Policy Working Group 2002: 2) as "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed." This definition connotes return to some previous condition, yet the plan explicitly says that return to a previous condition is not the goal. Finally, the plan adopts adaptive management as its *modus operandi*. Although conceived by Walters (1986) as a rigorous method with tests of hypotheses and clear criteria for rejection, this method is often applied operationally as "change it if it doesn't look like it's working" (Simberloff 1998). It will be important to bear in mind that for adaptive management to be truly scientific, it must entail quantification, replication, and stated criteria for rejecting hypotheses.

Acknowledgements

I thank J. Bender, J.-L. Martin, V. Nealis, G. Nugent, and R. Randall for information on particular projects and A.J. Gaston, T.E. Golumbia, and J.-L. Martin for comments on an early draft of this manuscript.

Literature cited

Anonymous. 1999. New moth a greater threat than tussock moth. Available at http://www.hortnet.co.nz/news/99/n3002.htm.

Baltzinger, C.; Martin, J.-L. 1998. The effect of browsing by deer on the regeneration of western red cedar in Haida Gwaii (Queen Charlotte Islands). Pages 42–65 *in* A.J. Gaston (ed.), Laskeek Bay Research 8. Laskeek Bay Conservation Society, Queen Charlotte City, B.C.

Barnard, J. 1999. Bug "team" sweeps Scotch broom. The Oregonian, 20 July, p. B4.

Baskin, Y. 2002. A plague of rats and rubbervines. Island Press, Washington, D.C.

Bax, N.; Hayes, K.; Marshall, A.; Parry, D.; Thresher, R. 2002. Man-made marinas as sheltered islands for alien marine organisms: Establishment and eradication of an alien invasive marine species. Pages 26–39 *in* C.R. Veitch and M.N. Clout (eds.), Turning the tide: The eradication of invasive species. Invasive Species Specialist Group, Species Survival Commission, World Conservation Union (IUCN), Gland, Switzerland.

Beck, K.G. 1999. Biennial thistles. Pages 145–161 *in* R.L. Sheley and J.K. Petroff (eds.), Biology and management of noxious rangeland weeds. Oregon State University Press, Corvallis, Oregon.

Bell, B.D. 1999. The good and bad news from Mauritius. Aliens 9: 6.

Bergström, R.; Bergqvist, G. 1997. Frequencies and patterns of browsing by large herbivores on conifer seedlings. Scand. J. For. Res. 12: 288–294.

Bossard, C.C. 1991. The role of habitat disturbance, seed predation and ant dispersal on establishment of the exotic shrub *Cytisus scoparius* in California. Am. Midl. Nat. 126: 1–13.

Bossard, C.C. 2000. *Cytisus scoparius* (L.) Link. Pages 145–150 *in* C.C. Bossard, J.M. Randall, and M.C. Hoshovsky (eds.), Invasive plants of California's wildlands. University of California Press, Berkeley, California.

Bourne, J. 2000. A history of rat control in Alberta. Alberta Agriculture, Food and Rural Development, Edmonton, Alberta.

Caley, P. 1993. Population dynamics of feral pigs (*Sus scrofa*) in a tropical riverine habitat complex. Wildl. Res. 20: 625–636.

Carson, R. 1962. Silent spring. Houghton Mifflin, Boston, Massachusetts.

Chapuis, J.-L.; Barnaud, G. 1995. Restauration d'îles de l'archipel de Kerguelen par éradication du lapin (*Oryctolagus cuniculus*): Méthode d'intervention appliquée sur l'Île Verte. Rev. Écol. (Terre Vie) 50: 377–390.

Clearwater, J.R. 2002. Tackling tussock moths: strategies, timelines and outcomes of two programs for eradicating tussock moths from suburbs of Auckland, New Zealand. Page 407 *in* C.R. Veitch and M.N. Clout (eds.), Turning the tide: The eradication of invasive species. Invasive Species Specialist Group, Species Survival Commission, World Conservation Union (IUCN), Gland, Switzerland.

Coblentz, B.E.; Baber, D.W. 1987. Biology and control of feral pigs on Isla Santiago, Galapagos, Ecuador. J. Appl. Ecol. 24: 403–418.

Crooks, J.; Soulé, M.E. 1996. Lag times in population explosions of invasive species: Causes and implications. Pages 39–46 *in* O.T. Sandlund, P.J. Schei, and A. Viken (eds.), Proceedings, Norway/United Nations conference on alien species. Directorate for Nature Management and Norwegian Institute for Nature Research, Trondheim, Norway.

Curtis, M. 1996. Community groups make a clean sweep to eliminate broom. Victoria Times-Colonist, 1 November, p. A4.

Dash, B.A.; Gliessman, S.R. 1994. Nonnative species eradication and native species enhancement: Fennel on Santa Cruz Island. Pages 505–512 *in* W.L. Halvorson and G.J. Maender (eds.), The fourth California islands symposium: Update on the status of resources. Santa Barbara Museum of Natural History, Santa Barbara, California.

Daufresne, T.; Martin, J.-L. 1997. Changes in vegetation structure and diversity in relation to the presence of a large herbivore: The impact of introduced black-tailed deer on old-growth forests in Haida Gwaii (Queen Charlotte Islands). Pages 2–26 *in* A.J. Gaston (ed.), Laskeek Bay Research 7. Laskeek Bay Conservation Society, Queen Charlotte City, B.C.

Davis, J.R.; Garcia, R. 1989. Malaria mosquito in Brazil. Pages 274–283 *in* D.L. Dahlsten and R. Garcia (eds.), Eradication of exotic pests. Yale University Press, New Haven, Connecticut.

Day, M.; Daltry, J. 1996a. Antiguan racer conservation project. Flora & Fauna News, April.

Day, M.; Daltry, J. 1996b. Rat eradication to conserve the Antiguan racer. Aliens 3: 14–15.

Day, M.; Hayes, W.; Varnham, K.; Ross, T.; Carey, E.; Ferguson, T.; Monestine, J.; Smith, S.; Armstrong, C.; Buckle, A.; Alberts, A.; Buckner, S. 1998. Rat eradication to protect the White Cay iguana. Aliens 8: 22–24.

deCalesta, D.S.; Stout, S.L. 1997. Relative deer density and sustainability: a conceptual framework for integrating deer management with ecosystem management. Wildl. Soc. Bull. 25: 252–258.

Desrochers, A.M.; Bain, J.F.; Warwick, S.I. 1988. The biology of Canadian weeds. 89. *Carduus nutans* L. and *Carduus acanthoides* L. Can. J. Plant Sci. 68: 1053–1068.

Diefenbach, D.R.; Palmer, W.L. 1997. Deer management: marketing the science. Wildl. Soc. Bull. 25: 378–381.

Dzięciolowski, R.M.; Clarke, C.M.H.; Frampton, C.M. 1992. Reproductive characteristics of feral pigs in New Zealand. Acta Theriol. 37: 259–270.

Econews. 1998. City wide broom bash. Newsletter No. 77 (serving Vancouver Island's environmental community), November. Available at http://www.earthfuture.com/econews/back_issues/98-11.htm.

Engelstoft, C. 2002a. Restoration priorities associated with introduced species impacts on Haida Gwaii/Queen Charlotte Islands: Perspectives and strategies. Section 2: Local perspectives. Terrestrial Ecosystems Restoration Program, Queen Charlotte City, B.C.

Engelstoft, C. 2002b. Restoration priorities associated with introduced species impacts on Haida Gwaii/Queen Charlotte Islands: Perspectives and strategies. Section 3: Strategic plan. Terrestrial Ecosystems Restoration Program, Queen Charlotte City, B.C.

Engelstoft, C.; Bland, L. 2002. Restoration priorities associated with introduced species impacts on Haida Gwaii/Queen Charlotte Islands: Perspectives and strategies. Section 1: Introduced species account. Terrestrial Ecosystems Restoration Program, Queen Charlotte City, B.C.

Fenner, F.; Henderson, D.A.; Arita, I.; Ježek, Z.; Ladnyi, I.D. 1988. Smallpox and its eradication. World Health Organization, Geneva, Switzerland.

Flint, E.; Rehkemper, C. 2002. Control and eradication of the introduced grass, *Cenchrus echinatus*, at Laysan Island, central Pacific Ocean. Pages 110–115 *in* C.R. Veitch and M.N. Clout (eds.), Turning the tide: The eradication of invasive species. Invasive Species Specialist Group, Species Survival Commission, World Conservation Union (IUCN), Gland, Switzerland.

Follett, P.A.; Duan, J.J. (eds.). 2000. Nontarget effects of biological control. Kluwer, Boston, Massachusetts.

Fraser, K.W. 2000. Status and conservation role of recreational hunting on conservation land. Science for Conservation 140, Department of Conservation, Wellington, New Zealand.

Fuller, R.J.; Gill, R.M.A. 2001. Ecological impacts of increasing numbers of deer in British woodland. Forestry 74: 193–199.

Gill, R.M.A. 1992a. A review of damage by mammals in north temperate forests. 1. Deer. Forestry 65: 145–169.

Gill, R.M.A. 1992b. A review of damage by mammals in north temperate forests. 3. Impact on trees and forests. Forestry 65: 363–388.

Gill, R.M.A.; Beardall, V. 2001. The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. Forestry 74: 209–218.

Golumbia, T.E. 2000. Introduced species management in Haida Gwaii (Queen Charlotte Islands). Pages 327–331 *in* L.M. Darling (ed.), Proceedings of a conference on the biology and management of species and habitats at risk, Kamloops, B.C., 15–19 February 1999. Vol. 1. B.C. Ministry of Environment, Lands, and Parks, Victoria, B.C.

Gordon, D.R.; Thomas, K.P. 1997. Florida's invasion by nonindigenous plants: History, screening, and regulation. Pages 21–37 *in* D. Simberloff, D.C. Schmitz, and T.C. Brown (eds.), Strangers in paradise. Impact and management of nonindigenous species in Florida. Island Press, Washington, D.C.

Greathead, D.J. 1995. Benefits and risks of classical biological control. Pages 53–63 *in* H.M.T. Hokkanen and J.M. Lynch (eds.), Biological control. Benefits and risks. Cambridge University Press, Cambridge, U.K.

Hendrickson, O. 2002. Invasive alien species in Canadian forests. Pages 59–71 *in* R. Claudi, P. Nantel, and E. Muckle-Jeffs (eds.), Alien invaders in Canada's waters, wetlands, and forests. Canadian Forest Service, Ottawa, Ontario.

Holbrook, S.H. 1943. Burning an empire. The story of American forest fires. Macmillan, New York.

Holubitsky, J. 2000. Any season is open season for these hunters. Edmonton Journal, 15 October, pp. A1, A7.

Hone, J.; Stone, C. 1989. A comparison and evaluation of feral pig management in two national parks. Wildl. Soc. Bull. 17: 419–425.

Hoshovsky, M. 2002. Element stewardship abstract for *Ulex europaeus*—gorse. The Nature Conservancy, Arlington, Virginia. Available at http://tncweeds.ucdavis.edu/esadocs/documnts/ulexeur.html.

Howald, G.R.; Mineau, P.; Elliott, J.E.; Cheng, K.M. 1999. Brodifacoum poisoning of avian scavengers during rat control on a seabird colony. Ecotoxicology 8: 431–447.

Kaiser, G.W.; Taylor, R.H.; Buck, P.D.; Elliott, J.E.; Howald, G.R.; Drever, M.C. 1997. The Langara Island Seabird Habitat Recovery Project: Eradication of Norway rats—1993–1997. Technical Report Series No. 304, Canadian Wildlife Service, Pacific and Yukon Region, Delta, B.C.

Katahira, L.K.; Finnegan, P.; Stone, C.P. 1993. Eradicating feral pigs in montane mesic habitat in Hawaii Volcanoes National Park. Wildl. Soc. Bull. 21: 269–274.

Kessler, C.C. 2002. Eradication of feral goats and pigs and consequences for other biota on Sarigan Island, Commonwealth of the Northern Mariana Islands. Pages 132–140 *in* C.R. Veitch and M.N. Clout (eds.), Turning the tide: The eradication of invasive species. Invasive Species Specialist Group, Species Survival Commission, World Conservation Union (IUCN), Gland, Switzerland.

Kirby, K.J. 2001. The impact of deer on the ground flora of British broadleaved woodland. Forestry 74: 219–229.

Lockwood, J.; Simberloff, D.; McKinney, M.; Von Holle, B. 2001. How many, and which, plants will invade natural areas? Biol. Invasions 3: 1–8.

Lonsdale, W.M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology 80: 1522–1536.

Louda, S.M. 2000. Negative ecological effects of the musk thistle biological control agent, *Rhinocyllus conicus*. Pages 215–243 *in* P.A. Follett and J.J. Duan (eds.), Nontarget effects of biological control. Kluwer, Boston, Massachusetts.

Louda, S.M.; Kendall, D.; Connor, J.; Simberloff, D. 1997. Ecological effects of an insect introduced for the biological control of weeds. Science 277: 1088–1090.

Markiw, M.E. 1992. Salmonid whirling disease. Fish and Wildlife Leaflet 17, Fish and Wildlife Service, U.S. Department of the Interior, Washington, D.C.

Martin, J.-L.; Baltzinger, C. 2002. Interaction among deer browsing, hunting, and tree regeneration. Can. J. For. Res. 32: 1254–1264.

Martin, J.-L.; Joron, M.; Gaston, A.J. 2001. The squirrel connection: influence of squirrels as songbird nest predators in Laskeek Bay. Pages 43–60 *in* A.J. Gaston (ed.), Laskeek Bay Research 10. Laskeek Bay Conservation Society, Laskeek Bay Conservation Society, Queen Charlotte City, B.C.

McFadyen, R.E.C. 1998. Biological control of weeds. Annu. Rev. Entomol. 43: 369–393.

Meinesz, A. 2001. Killer algae. University of Chicago Press, Chicago, Illinois.

Micol, T.; Jouventin, P. 2002. Eradication of rats and rabbits from Saint-Paul Island, French Southern Territories. Pages 199–205 *in* C.R. Veitch and M.N. Clout (eds.), Turning the tide: The eradication of invasive species. Invasive Species Specialist Group, Species Survival Commission, World Conservation Union (IUCN), Gland, Switzerland.

Miller, J.C. 1990. Field assessment of the effects of a microbial pest control agent on nontarget Lepidoptera. Am. Entomol. 36: 135–139.

Myers, J.H.; Simberloff, D.; Kuris, A.M.; Carey, J.R. 2000. Eradication revisited: dealing with exotic species. Trends Ecol. Evol. 15: 316–320.

Nealis, V.G. 2002. Gypsy moth in Canada: Case study of an invasive insect. Pages 151–159 *in* R. Claudi, P. Nantel, and E. Muckle-Jeffs (eds.), Alien invaders in Canada's waters, wetlands, and forests. Canadian Forest Service, Ottawa, Ontario.

New Zealand Department of Conservation. 2002. http://www.doc.govt.nz/Regional-Info/008~Wellington/001~Kapiti-Island-Nature-Reserve.asp (accessed 20 July 2002).

New Zealand Ministry of Agriculture and Forestry. 1998. MAF places precautionary tussock moth traps. Available at http://www.maf.govt.nz/MAFnet/press/091198mth.htm (accessed 15 July 2002).

New Zealand Parliamentary Commissioner for the Environment. 2000. New Zealand under siege: A review of the management of biosecurity risks to the environment. Wellington, New Zealand.

Nickum, D. 1999. Whirling disease in the United States. A summary of progress in research and management. Trout Unlimited, Arlington, Virginia.

Nugent, G.; Fraser, K.W.; Asher, G.W.; Tustin, K.G. 2001. Advances in New Zealand mammalogy 1990–2000: Deer. J. R. Soc. New Zeal. 31: 263–298.

Pascal, M. 1996. Norway rat eradication from Brittany islands. Aliens 3: 15.

Pascal, M.; Siorat, F.; Bernard, F. 1998. Norway rat and shrew interactions: Brittany. Aliens 7: 8.

Pojar, J.; Banner, A. 1984. Old-growth forests and introduced black-tailed deer on the Queen Charlotte Islands, British Columbia. Pages 247–257 *in* W.R. Meehan, T.R. Merrell, Jr., and T.A. Hanley (eds.), Fish and wildlife relationships in old-growth forests: Proceedings of a symposium held in Juneau, Alaska, 12–15 April 1982. American Institute of Fishery Research Biologists, Morehead City, North Carolina.

Prasad, R. 2001. Scotch broom, *Cytisus scoparius* L. in British Columbia. Pacific Forestry Centre, Canadian Forest Service, Victoria, B.C. Available at http://www.pfc.cfs.nrcan.gc.ca/biodiversity/broom%5Fe.html.

Randall, R. 2001. Eradication of a deliberately introduced plant found to be invasive. Page 174 *in* R. Wittenberg and M.J.W. Cock (eds.), Invasive alien species: A toolkit of best prevention and management practices. CAB International, Wallingford, Oxon, U.K.

Rejmánek, M.; Pitcairn, M.J. 2002. When is eradication of exotic pest plants a realistic goal? Pages 249–253 *in* C.R. Veitch and M.N. Clout (eds.), Turning the tide: The eradication of invasive species. Invasive Species Specialist Group, Species Survival Commission, World Conservation Union (IUCN), Gland, Switzerland.

Rejmánek, M.; Richardson, D.M. 1996. What attributes make some plant species more invasive? Ecology 77: 1655–1661.

Rooney, T.P. 2001. Deer impacts on forest ecosystems: a North American perspective. Forestry 74: 201–208.

Sakai, A.K.; Allendorf, F.W.; Holt, J.S.; Lodge, D.M.; Molofsky, J.; With, K.A.; Baughman, S.; Cabin, R.J.; Cohen, J.E.; Ellstrand, N.C.; McCauley, D.E.; O'Neil, P.; Parker, I.M.; Thompson, J.N.; Weller, S.G. 2001. The population biology of invasive species. Annu. Rev. Ecol. Syst. 32: 305–332.

Sample, B.E.; Butler, L.; Whitmore, R.C. 1992. The impacts of *Bacillus thuringiensis* applications on non-target arthropods: Preliminary results. Appalachian Gypsy Moth Integrated Pest Management Project (AIPM) Demonstration Project News 5(7): 1–4.

Schmitz, D.C.; Simberloff, D. 1997. Biological invasions: a growing threat. Issues Sci. Technol. 13(4): 33–40.

Schuyler, P.T.; Garcelon, D.; Escover, S. 2002. Eradication of feral pigs (*Sus scrofa*) on Santa Catalina Island, California, U.S.A. Pages 274–286 *in* C.R. Veitch and M.N. Clout (eds.), Turning the tide: The eradication of invasive species. Invasive Species Specialist Group, Species Survival Commission, World Conservation Union (IUCN), Gland, Switzerland.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? Biol. Conserv. 83: 247–257.

Simberloff, D. 2000. Nonindigenous species: a global threat to biodiversity and stability. Pages 325–334 *in* P. Raven and T. Williams (eds.), Nature and human society: The quest for a sustainable world. National Academy Press, Washington, D.C.

Simberloff, D. 2001. Biological invasions—How are they affecting us, and what can we do about them? West. N. Am. Nat. 61: 308–315.

Simberloff, D. 2002a. Managing established populations of alien species. Pages 269–278 *in* R. Claudi, P. Nantel, and E. Muckle-Jeffs (eds.), Alien invaders in Canada's waters, wetlands, and forests. Canadian Forest Service, Ottawa, Ontario.

Simberloff, D. 2002b. Today Tiritiri Matangi, tomorrow the world!—Are we aiming too low in invasives control? Pages 4–12 *in* C.R. Veitch and M.N. Clout (eds.), Turning the tide: The eradication of invasive species. Invasive Species Specialist Group, Species Survival Commission, World Conservation Union (IUCN), Gland, Switzerland.

Simberloff, D. 2003. How much population biology is needed to manage introduced species? Conserv. Biol. 17: 1–11.

Simberloff, D.; Alexander, M. 1998. Assessing risks to ecological systems from biological introductions (excluding genetically modified organisms). Pages 147–176 *in* P. Calow (ed.), Handbook of environmental risk assessment and management. Blackwell, Oxford, U.K.

Simberloff, D.; Stiling, P.D. 1996. How risky is biological control? Ecology 77: 1965–1974.

Simberloff, D.; Von Holle, M. 1999. Positive interactions of nonindigenous species: invasional meltdown? Biol. Invasions 1: 21–32.

Society for Ecological Restoration International. 2002. http://www.ser.org/definitions.html (accessed 5 July 2002).

Society for Ecological Restoration International Science & Policy Working Group. 2002. The SER International primer on ecological restoration. Available at http://www.ser.org/content/ecological_restoration_primer.asp (accessed 29 July 2002).

Taylor, R.H.; Kaiser, G.W.; Drever, M.C. 2000. Eradication of Norway rats for recovery of seabird habitat on Langara Island, British Columbia. Restor. Ecol. 8: 151–160.

Tershy, B.R.; Donlan, C.J.; Keitt, B.S.; Croll, D.A.; Sanchez, J.A.; Wood, B.; Hermosillo, M.A.; Howald, G.R.; Biavaschi, N. 2002. Island conservation in north-west Mexico: a conservation model integrating research, education, and exotic mammal eradication. Pages 293–300 *in* C.R. Veitch and M.N. Clout (eds.), Turning the tide: The eradication of invasive species. Invasive Species Specialist Group, Species Survival Commission, World Conservation Union (IUCN), Gland, Switzerland.

Timmins, S.M.; Braithwaite, H. 2002. Early detection of new invasive weeds on islands. Pages 311–318 *in* C.R. Veitch and M.N. Clout (eds.), Turning the tide: The eradication of invasive species. Invasive Species Specialist Group, Species Survival Commission, World Conservation Union (IUCN), Gland, Switzerland.

Towns, D.R.; Simberloff, D.; Atkinson, I.A.E. 1997. Restoration of New Zealand islands: redressing the effects of introduced species. Pac. Conserv. Biol. 3: 99–124.

U.S. Department of the Interior (Fish and Wildlife Service). 1997. Endangered and threatened wildlife and plants; determination of Endangered status for two tidal marsh plants—*Cirsium hydrophilum* var. *hydrophilum* (Suisun Thistle) and *Cordylanthus mollis* ssp. *mollis* (Soft Bird's-Beak) from the San Francisco Bay area of California. 50 CFR Part 17. Fed. Regist. 62(224): 61916–61921.

U.S. National Invasive Species Council. 2001. Management plan. Meeting the invasive species challenge. 18 January. Available at http://www.invasivespecies.gov/council/mp.pdf.

U.S. National Research Council. 2000. Incorporating science, economics, and sociology in developing sanitary and phytosanitary standards in international trade. National Academy Press, Washington, D.C.

Varnham, K.; Ross, T.; Daltry, J.; Day, M. 1998. Recovery of the Antiguan racer. Aliens 8: 21.

Veitch, C.R. 2002. Eradication of Pacific rats (*Rattus exulans*) from Tiritiri Matangi Island, Hauraki Gulf, New Zealand. Pages 360–364 *in* C.R. Veitch and M.N. Clout (eds.), Turning the tide: The eradication of invasive species. Invasive Species Specialist Group, Species Survival Commission, World Conservation Union (IUCN), Gland, Switzerland.

Veitch, C.R.; Bell, B.D. 1990. Eradication of introduced animals from the islands of New Zealand. Pages 137–146 *in* D.R. Towns, C.H. Daugherty, and I.A.E. Atkinson (eds.), Ecological restoration of New Zealand islands. Department of Conservation, Wellington, New Zealand.

Veitch, C.R.; Clout, M.N. (eds.). 2002. Turning the tide: The eradication of invasive species. Invasive Species Specialist Group, Species Survival Commission, World Conservation Union (IUCN), Gland, Switzerland.

Victor, D.G. 2000. Risk management and the world trading system: Regulating international trade distortions caused by national sanitary and phytosanitary policies. Pages 118–169 *in* U.S. National Research Council, Incorporating science, economics, and sociology in developing sanitary and phytosanitary standards in international trade. National Academy Press, Washington, D.C.

Vila, B.; Guibal, F.; Torre, F.; Martin, J.L. 2003. Growth change of young *Picea sitchensis* in response to deer browsing. For. Ecol. Manage. 180: 413–424.

Walters, C.J. 1986. Adapative management of renewable resources. Macmillan, New York.

Westbrooks, R.G.; Hayes, D.C.; Gregg, W.P. 2000. Proposed strategies for early detection, reporting, rapid assessment, and rapid response to new invasive plants in the United States of America. *In* Proceedings of a workshop, Federal Interagency Committee for the Management of Noxious and Exotic Weeds, Washington, D.C.

Williams, T. 1997. Killer weeds. Audubon 99(2): 24–31.

Williamson, M. 1996. Biological invasions. Chapman & Hall, London, U.K.

Williamson, M.; Brown, K.C. 1986. The analysis and modelling of British invasions. Phil. Trans. R. Soc. B 314: 505–522.

Wood, B.; Tershy, B.R.; Hermosillo, M.A.; Donlan, C.J.; Sanchez, J.A.; Keitt, B.S.; Croll, D.A.; Howald, G.R.; Biavaschi, N. 2002. Removing cats from islands in north-west Mexico. Pages 374–380 *in* C.R. Veitch and M.N. Clout (eds.), Turning the tide: The eradication of invasive species. Invasive Species Specialist Group, Species Survival Commission, World Conservation Union (IUCN), Gland, Switzerland.

Zavaleta, E.; Hobbs, R.; Mooney, H. 2001. Putting invasive species removal in a whole-ecosystem context. Trends Ecol. Evol. 16: 454–459.

White-tailed deer impacts in North America and the challenge of managing a hyperabundant herbivore

Donald M. Waller

Abstract

Like other large ungulates, white-tailed deer *Odocoileus virginianus* declined to the point of extirpation across much of eastern and central North America by the end of the 19th century. Deer populations then rebounded strongly in response to changed cultural conditions (effective game protection laws) combined with pervasive changes in ecological conditions (early successional habitats with scarce predators and competitors). This spectacular rebound continued through most of the 20th century, boosted by active game management activities, recreational feeding of deer, and mild winters. Deer now exist at record densities across much of their range and are exerting complex and cascading effects on natural ecosystems. These effects can mirror those of deer introduced onto islands in terms of their extent and severity but are often underestimated due to poor baseline data, few "controls," and inadequate monitoring. Studies using exclosures, island comparisons, or demography reveal that deer are dramatically reducing the regeneration of many shrubs and trees, including conifer (Canada yew *Taxus canadensis*, northern white cedar *Thuja occidentalis*, eastern hemlock *Tsuga canadensis*, and white pine *Pinus strobus*) and hardwood species (e.g., northern red oak *Quercus rubra* and yellow birch *Betula allegheniensis*). The loss of cover adversely affects some understory birds. Impacts on herbaceous understory communities are harder to assess, but are substantial in many areas. Comparisons of habitats with and without deer and resurveys of areas with accurate historical baseline data indicate that high deer densities simplify and homogenize herb communities. Orchids, some lilies, and other rare plants are particularly likely to decline in deer-dominated landscapes. Species losses can exceed 50%, even in parks, if deer hunting is prohibited. Areas like Native American reservations in the United States that support fewer deer have healthy patterns of tree regeneration. Deer can also foster the invasion of weedy exotics. Many of these impacts appear difficult to reverse and could persist for decades or centuries. Despite clear evidence that deer densities need to be reduced, deer and forest managers face difficult issues, including how to adapt hunting regulations and incentives, restricted access to private lands, and outbreaks of deer-borne diseases. Because we continue to discover new impacts of overabundant deer and because these impacts appear pervasive and long-lasting, we need more comprehensive research and monitoring programs. Research and monitoring results could also assist management agencies in making and implementing difficult decisions, particularly if efforts were better coordinated across regions and better integrated into decision-making via adaptive management.

1. Introduction: Deer—Dr. Jeckyl or Mr. Hyde?

Deer are special. They are respected as perhaps the most popular game animal, appreciated as an important source of wild meat, and widely revered among both hunters and nonhunters as a symbol of wild beauty. The high popularity of deer hunting and accompanying licensing revenues represent the financial backbone of many wildlife management programs. These programs, in turn, have worked hard to sustain and, in some cases, increase populations of deer via habitat management programs. The popularity of deer with nonhunters also exerts strong economic and ecological influences, as wildlife viewing continues to climb in popularity and the public avidly buys and distributes ever-greater quantities of supplemental deer feed.

However, ever more deer may not be beneficial. Soaring deer populations have contributed to epidemics of new diseases, high agricultural losses, failures in tree regeneration, and ever-increasing accidents with vehicles. Communities across North America must now wrestle with these contradictory aspects of deer management. In choosing how best to manage introduced Sitka black-tailed deer *Odocoileus hemionus sitkensis* in Haida Gwaii (Queen Charlotte Islands, British Columbia), it is worth contemplating how management choices made in other parts of North America have played out over time. This paper, therefore, provides an overview of deer population trends in mainland North America and the cumulative impacts of these trends on the ecological conditions of forests. I concentrate on forests of the eastern and central United States and white-tailed deer *Odocoileus virginianus*, as our understanding of deer impacts has progressed in this region.

I first review historical shifts in forest and wildlife management that led to the chronically high deer populations we see today. I then summarize some of what we know about the many ways in which dense deer populations are affecting these forest ecosystems and describe the various methods

that are used to infer impacts. Known impacts now include reductions in tree seedling recruitment, shrub and sapling cover, altered patterns of bird and mammal abundance, and reduced herb species diversity. Each of these is described in turn. Collectively, the results point to a need to limit deer densities and continuously monitor their impacts. Managers, however, must often act without accurate local information regarding deer impacts. They also face a complex set of biological, social, and economic factors that constrain their ability to manage deer quickly and effectively. These, too, deserve our consideration if we are to better integrate research and monitoring with deer management, as discussed in the final section. As this review is necessarily brief, readers should also consult other reviews on the ecological impacts of deer in North America (Alverson et al. 1988; Tilghman 1989; Hadidian 1993; McShea et al. 1997; Waller and Alverson 1997; Rooney 2001) and ungulates in Europe (special issue of Forestry, 2001, Volume 74, Number 3).

2. Why are deer populations so high?

How did white-tailed deer densities increase to the hyperabundant levels we find today in much of North America? Following European settlement, a complex cascade of ecological, social, and economic changes occurred that interacted to greatly affect mammal densities throughout the northeast (Cronon 1983; Williams 1989). Most obviously, all the large ungulates were heavily hunted, first for subsistence and later to serve growing markets for wild meat. Deer, as the most abundant and widespread ungulate in North America, were the focus for much of this hunting. Hunting pressure vastly diminished deer populations along the eastern seaboard by the early 19th century, extirpating them from several New England and central Atlantic states. These reductions spread to the agricultural and forested regions of the Midwest by the late 19th century. The same human hunting that decimated deer had even greater effects on bison *Bison bison*, elk *Cervus elaphus*, moose *Alces alces*, and caribou *Rangifer tarandus*. Although each tended to predominate in a different habitat, these larger ungulates proved even more sensitive to hunting than deer, as they grow and reproduce more slowly.

These declines in ungulate density had cascading effects on other species. Most obviously, fewer ungulates meant a contracting prey base for native large mammalian carnivores, such as the cougar *Puma concolor*, wolf *Canis lupus*, and wolverine *Gulo gulo*. At the same time, these carnivores were ruthlessly hunted and trapped as "varmints" believed to threaten livestock, wild game, and potentially human life. They, too, were systematically extirpated in a rolling wave that followed patterns of European settlement across North America in the 18th and 19th centuries. Unlike ungulates, however, the persecution of predators continued far into the 20th century. Large mammalian predators remain scarce or absent across most of the eastern and central continental United States. Native American hunters of deer also suffered massive displacement and extirpation, first via disease and later from wars.

Thus, most major predators of deer other than humans were extirpated by the early 20th century, and populations of other ungulate potential competitors were also greatly diminished. At this point, the conspicuous power of market hunting to deplete populations of wildlife and the widespread decline or loss of game populations led to the enactment of strict game and wildlife protection laws (Fox 1981). These laws protect populations by strictly limiting hunting seasons (typically to 9–14 days during the fall rut) and by favouring buck hunting over the hunting of does. As these game protection laws became universal, the stage was set for the dramatic rebound in deer populations that continued through most of the 20th century.

The 20th century rebound in deer populations was accentuated by the widespread changes that occurred in North American landscapes (Alverson et al. 1994). The wave of loggers that spread across North America quickly felled the old-growth stands that predominated on forested landscapes. Lands not converted to agriculture or pasture regrew as younger successional stands, often to be cut a second or third time by the late 20th century. As logging replaced blow-downs, ice storms, and the occasional fire as the dominant mode of disturbance in forested landscapes, the matrix was inverted. The predominantly old-growth forests with interspersed small- to medium-sized openings and scattered early successional patches provided only occasional patches of forage for white-tailed deer. In contrast, the repeatedly logged forests that dominate eastern and central North American forests today are predominantly young stands with a preponderance of the open and edge habitats that favour deer (Leopold 1933; Alverson et al. 1988). Many public and industrial private forestlands in the Great Lake States, for example, are now managed to produce aspen *Populus*, a premier early successional species known to support deer populations and one that is rarely allowed to mature beyond 35 or 40 years, for paper pulp. In addition, game and forest managers also strove to actively maintain "wildlife openings" and the edge habitats to sustain high deer densities. Deer populations in the Great Lake States increase in direct proportion to the amount of early successional habitat and openings in their environment (McCaffery 1986).

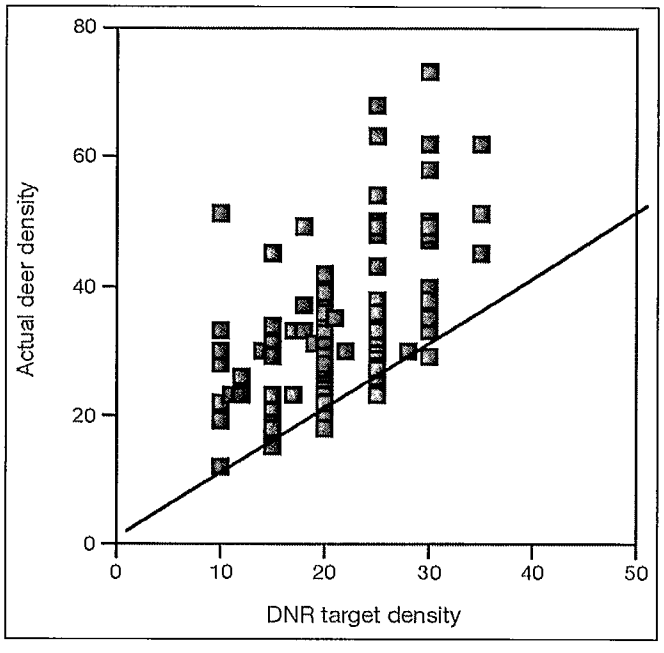
Many logged areas were quickly converted to the agricultural landscapes that now dominate lowlands in the east and the central plains. These areas support a matrix of mostly farm fields and pastures and ever-increasing suburban areas that often support deer habitat in the form of scattered woodlot "islands." Such edge-rich environments also favour deer eager to consume crop residues, pasture grasses, and horticultural plantings. Deer populations in the late 20th century were boosted even further in many regions by two other factors. First, many residents in suburban and rural areas began to feed on deer in large numbers, and hunters also increased their use of feed as bait. The sale and distribution of deer feed supplements quickly grew into a major industry involving millions of bushels of corn, potatoes, and other feeds just in Wisconsin (K. McCaffery, pers. commun.). Although such supplemental feeding can act to reduce local deer browse impacts (at least temporarily; Doenier et al. 1997), it tends to increase browse impacts overall by boosting deer densities, particularly in the north of their range, where food resources tend to limit overwinter survival. Many people who enjoy feeding and watching deer also post their land against hunting, limiting the cull and thus boosting deer populations. Finally, this period also recorded

many of the mildest winters on record, further favouring overwinter survival, particularly near the northern limit of their range.

Thus, game protection laws, the loss of native predators, and intensive and extensive patterns of forest management acted together to boost white-tailed deer populations to levels far higher than those that prevailed before European settlement. Deer now exist at chronically high densities throughout most of eastern, southern, and central North America. In northern Wisconsin, for example, deer are thought to have occurred at a density of 2–5 overwintering deer per square kilometre of suitable habitat before European settlement (McCabe and McCabe 1984) but now range from 8 to over 20 deer per square kilometre through most this region (Garrott et al. 1993). Densities in southern Wisconsin are even higher, so deer densities exceed, sometimes greatly, "target" densities set by the Wisconsin Department of Natural Resources in almost every Deer Management Unit (Fig. 1). Similar situations exist in most eastern and midwestern states, with densities exceeding 20/km^2 in many suburban areas.

While the recovery of white-tailed deer represents an obvious conservation success, wildlife managers now face the problems posed by an excess of success. As deer densities mount, wildlife managers are faced with trying to limit the Mr. Hyde side of deer impacts by reversing decades of effort devoted to boosting deer populations. This is proving difficult, making it all the more important to carefully document the effects that deer are having on native ecosystems.

Figure 1
Actual deer densities, as estimated by the Wisconsin Department of Natural Resources (DNR), plotted against management objective ("target") deer densities for the 117 Deer Management Units in Wisconsin in 2000. Units are the number of overwintering deer per square mile of habitat suitable for deer. One square mile = 2.53 km^2.



3. Deer impacts on forest ecosystems

3.1 Early indications of deer impacts

Evidence of the ecological impacts of ungulates on forests has been accumulating since the turn of the 20th century (Lutz 1930; Aldous 1941). The pioneer wildlife ecologist Aldo Leopold recognized the profound impacts that ungulate grazing could have on plant communities. This insight surely rested in part on observing the dramatic effects of overgrazing from cattle *Bos taurus* and mule deer *Odocoileus hemionus* in the southwestern United States. His understanding was sharpened by trips in the 1930s to regions of northern Mexico that lacked intense grazing and still supported wolves and cougars (Meine 1988). A trip to Germany and Austria in 1935–1936 similarly sharpened his sensitivity to the severe effects that deer could have on forests (Leopold 1936). This trip may have marked a turning point in 20th-century wildlife management: Leopold returned to decry the dangers of hyperabundant deer. In Europe, Leopold observed how overzealous forest management had led to "spruce mania" and how overzealous game management led to "Devonian forests" dominated by conifers in the overstory and browse-resistant ferns in the understory. He surmised that highly managed systems that focused on single products resulted in artificial forests incapable of sustaining full complements of wildlife and plant species. This pivotal experience led Leopold to campaign against the dangers in North America of managing forests and wildlife too intensively and without regard for the wider system (Leopold 1943, 1946). He also then worked to document the impacts of overabundant deer, encouraging research based on exclosures and measures of deer nutrition. He also realized the need to sway management policies on deer and so expended considerable effort to reform policies still predicated on increasing and protecting the herd. These efforts were only partly successful, eliciting more antagonism than understanding from many skeptical hunters (Meine 1988). Leopold's warnings about overabundant deer were widely ignored for the next 50 years, allowing Wisconsin's peak deer densities of the 1940s to return in the 1980s and 1990s.

Many observations of deer impacts were anecdotal, limited to particular years or sites, leading many to discount the general problem of deer overabundance. Impacts on trees and herbs in the Allegheny region of Pennsylvania, however, had become obvious by the 1970s (Healy 1971; Marquis 1975, 1981). Similar impacts were documented at that time for eastern hemlock *Tsuga canadensis* and northern white cedar *Thuja occidentalis* stands in Wisconsin (Blewett 1976; Anderson and Loucks 1979). A decade later, my own group reviewed the growing evidence for major deer impacts on a wide set of herbs and trees (Alverson et al. 1988). By the 1990s, the U.S. National Park Service had convened a special symposium on the topic (Warren 1991). Skepticism, however, remained high. Exclosure results, for example, were considered misleading, because they were often placed in deer yards known to support high densities of deer and represented an extreme, artificial condition of no deer. However, by the late 1990s, the tide of scientific opinion (at least) had turned, and issues surrounding deer overabundance

began to receive more attention. The Smithsonian Institution sponsored a special meeting and symposium volume on the issues (McShea et al. 1997), and the North American Wildlife Society dedicated a special issue of its Bulletin (1997, Volume 25, Number 2) to the problem. This accumulation of scientific evidence, however, has yet to convincingly sway public opinion and deer management policies in many regions. Reports of excessive tree browsing or wildflower losses are still often dismissed as isolated or anecdotal. Such reactions led us and others to seek more systematic and quantitative data on deer impacts that would remove lingering doubts.

3.2 How do we assess deer impacts?

To assess the impacts of deer on plant and animal communities, scientists employ a diversity of approaches. As noted above, fenced exclosures are clearly an effective way to compare areas without deer with surrounding "control" areas subject to ambient deer densities. Such exclosure studies demonstrate, often in a graphic way, just how strongly deer browsing can affect plant growth and tree regeneration. Such studies have existed for more than 50 years and continue to be actively employed to assess deer impacts (Graham 1958; Kroll et al. 1988; Stewart and Burrows 1989; Allison 1990a; Anderson and Katz 1993; Zimmermann 1995, 2000; Ruhren and Dudash 1996; Alverson and Waller 1997; Augustine and Frelich 1998). To be most useful for assessing deer effects, such exclosures should be built to exclude only deer and not hare or other mammals that can also affect plant growth and survival. Fenced areas can also be used to enclose deer at known densities to experimentally assess deer effects at levels other than zero and ambient densities (e.g., McShea and Rappole 1997). McCullough's (1984) work in the George Reserve in southern Michigan used a fenced area to assess the dynamics of deer populations and impacts.

Islands with and without deer or with deer at known densities can be used in a manner analogous to fenced exclosures to assess deer impacts in some regions. Island studies are particularly informative when many islands that can be used as replicates exist and when their histories of deer occupancy are known. Successful examples include studies of the vegetation and plant diversity on the Apostle Islands in Lake Superior (Beals et al. 1960; Balgooyen and Waller 1995). Work in Haida Gwaii (Queen Charlotte Islands, British Columbia) is taking particular advantage of the island approach to examine impacts of the now-abundant introduced Sitka black-tailed deer, and how quickly forests can recover from such effects (Martin and Baltzinger 2002; Stockton this volume). Islands have also been used to assess how variation in deer densities affects the abundance of insect vectors of human disease (Wilson et al. 1985).

Demography represents a useful third technique for assessing the impacts of deer on perennial plants. Most obviously, the number of seedlings and small saplings can be enumerated and compared with the abundance of larger size classes among stands known or thought to differ in deer browse intensity (e.g., Anderson and Loucks 1979). Such demographic profiles provide a clear picture of how deer can eliminate trees sensitive to browsing (Blewett 1976). They can also be used to chart improving tree regeneration once deer browse pressure declines (Anderson and Katz 1993). Extending this approach, the number of seedlings and saplings in progressively larger size classes can be used to examine how different biotic and abiotic environmental factors combine to affect seedling establishment and survival to subsequent size classes. We have used these approaches to examine the detailed patterns of recruitment in eastern hemlock and northern white cedar in Wisconsin (Waller et al. 1996; Rooney et al. 2002). Several such analyses can be combined into an overall path analysis to evaluate the relative strength of various factors on tree survival over successive size classes (Fig. 2). Comparisons of the size or age structure of herbs among areas with higher and lower deer densities can also be used to infer deer impacts (Anderson 1994; Rooney 1997; Rooney and Waller 2001). Such techniques deserve to be used more extensively in studies of deer impacts.

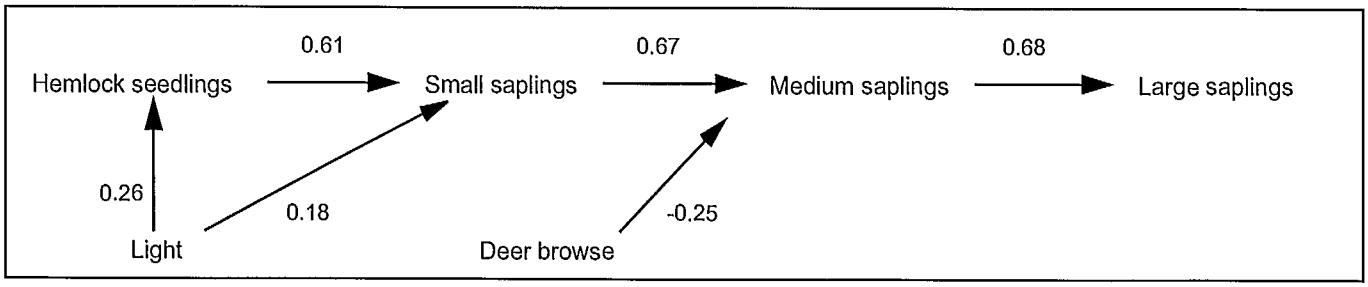
Finally, one may also use direct historical studies to track how populations or whole communities change over time in response to varying deer densities. Such "then versus now" studies require first a reliable source of baseline data that can be used to infer change. If it is assumed that such a baseline exists, these approaches further require some way of inferring whether the historical changes detected are indeed the result of deer impacts. Here, various approaches are possible. For example, one can compare two areas, otherwise similar, where one is known to have experienced high or increasing deer densities and the other supports fewer or declining numbers of deer. If the former community lost more species or experienced a transition to more deer-resistant species, it seems likely that such changes could be the result of deer. Even without such a "control" area, one might still infer deer impacts from changes in the relative abundances of species known to be resistant, or susceptible, to deer browsing. That is, if species known to be sensitive to deer herbivory (e.g., orchids and many lilies) experience systematic declines in an area harbouring moderate to high deer densities, whereas species known to resist herbivory (e.g., some ferns and most grasses and sedges) remain abundant or increase in abundance, it seems plausible that deer may be having systematic effects on the plant community. Miller et al. (1992) enumerated many rare plants thought to be sensitive to deer herbivory. We are exploiting these approaches to assess deer impacts in northern Wisconsin (Rooney et al. 2004).

3.3 Deer impacts on trees and shrubs

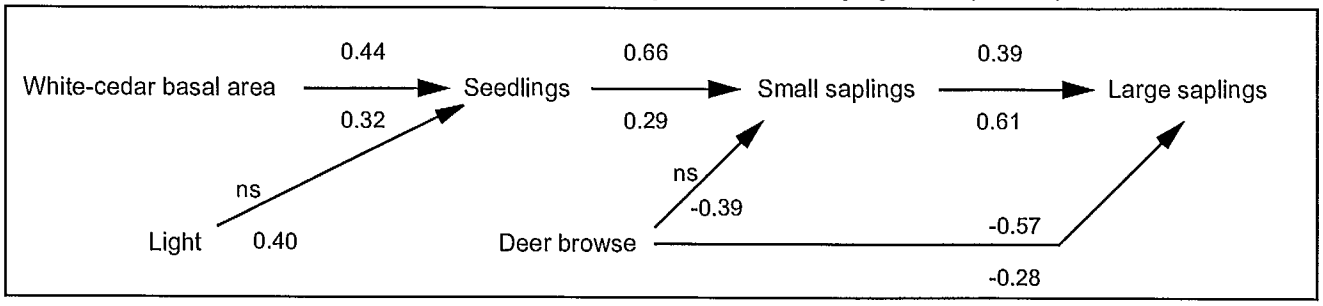
The fact that deer can have major impacts on the growth and survival of tree seedlings has been recognized for many years (Leopold et al. 1947; Webb et al. 1956). Forestry curricula and textbooks (e.g., Allen and Sharpe 1960) routinely mention that deer can restrict the regeneration of valuable timber species, such as many species of oak (*Quercus*). Deer often favour particular species for browse. In winter, deer in northern regions prefer evergreens such as Canada yew *Taxus canadensis*, eastern hemlock, and northern white cedar. Early work with exclosures (Graham 1958) and deer-free islands (Beals et al. 1960) in Wisconsin provided clear evidence of deer impacts on these favoured

Figure 2
Path diagrams of tree seedling demography in a) eastern hemlock *Tsuga canadensis* and b) northern white cedar *Thuja occidentalis*. Path analysis can integrate the effects of many predictor variables and graphically summarize the results of successive multivariate analyses. Such analyses consistently reveal that deer browsing curtails sapling recruitment in these species.

a) Path diagram for successive seedling size classes in eastern hemlock



b) Path diagram for successive seedling size classes in northern white cedar. Numbers above arrows are path coefficients from 1990–1991 data, and numbers below arrows are 1996 path coefficients. Direct paths not statistically significant ($P < 0:05$) are denoted as "ns".



browse species. Work in Scotland reveals that severe ungulate impacts on pine (*Pinus* spp.) regeneration can persist for hundreds of years (Watson 1983). Impacts on browsed trees are obvious to most field ecologists and foresters in terms of reduced numbers and sizes of seedlings and the shorn and torn twigs diagnostic of deer browsing. Such studies, however, have been criticized for being restricted to particular locations or for not paying attention to factors that affect seedling growth and survival at different stages (Mladenoff and Stearns 1993). Most tree regeneration studies focus on fine spatial scales, single causal variables, and/or only one stage of development (Clark et al. 1999). This makes it important to study and consider how other biotic and environmental factors might be affecting seedlings and to evaluate dynamics across a range of size or age classes (Waller et al. 1996). Deer impacts can also be complex, in that they can depend on both herbivore and seedling densities (Gill 1992).

Foresters in the Allegheny region of Pennsylvania have collected some of the most thorough and continuous data on how deer browsing affects patterns of tree regeneration (Harlow and Downing 1970; Marquis 1974, 1981; Tilghman 1989). Here, deer herds recovered in the 1930s and exceeded 20 deer/km^2 by 1960. Since then, browsing on hemlock, oaks, and other species has steadily favoured American beech *Fagus grandifolia*. Shrubs like hobblebush *Viburnum alnifolium* have also been strongly affected (Hough 1965). In some areas, browsing is intense enough to eliminate all tree regeneration, resulting in the production of stands with increasingly open understories dominated by grasses and ferns, termed "fern parks" by locals. Once established, these dense swards themselves interfere with tree regeneration (Horsley and Marquis 1983), indicating how deer can have indirect, as well as direct, effects (Waller and Alverson 1997; Rooney and Waller 2003).

Eastern hemlock seedlings are particularly susceptible to deer browse because they are favoured as winter browse and grow slowly (Curtis 1959; Hough 1965; Anderson and Loucks 1979; Frelich and Lorimer 1985; Alverson et al. 1988). This long-lived, shade-tolerant conifer favours moist sites and was distributed as a dominant or codominant tree across a broad region stretching from northeastern Minnesota through the Great Lakes region into southern Canada, New England, and south in mountains to the Carolinas (Nichols 1935; Braun 1950). Hemlock was an important component of Great Lake States forests for the last 3000 years (Davis 1987), but logging has now eliminated >99% of these hemlock forests (Eckstein 1980). The hardwood forests that replaced the original forests are far less hospitable for hemlock seedling regeneration, but recruitment has also been low, even in remnant hemlock stands (Curtis 1959; Frelich et al. 1993; Mladenoff and Stearns 1993). These levels are insufficient to maintain this cover type (Frelich and Lorimer 1985; Frelich and Reich 1995). Our own surveys of 100 hemlock stands throughout the region used four sequential size classes to assess the factors thought to limit seedling establishment and subsequent recruitment. Initial hemlock seedling establishment occurs in most stands and varies in response to overstory composition, light levels, and seedbed conditions (Rooney and Waller 1998). Recruitment to larger size classes, however, appears unrelated to light and geographic factors, but declines conspicuously with increases in estimated levels of deer browsing (Rooney et al. 2000). Multivariate statistical analyses of the factors affecting seedling and sapling abundance in each size class can be graphically summarized

in the form of a path analysis (Fig. 2a). These results demonstrate that restoring hemlock populations requires both (1) appropriate microsites for seedling establishment and (2) protection from excessive browse for successful recruitment. We also experimentally demonstrated the importance of deer browsing by erecting exclosures at 60 of these sites. These reveal a direct relationship between declines in the growth and survival of transplanted hemlock seedlings and declines estimates of local deer, but not hare, densities (Alverson and Waller 1997). Thus, restoring hemlock to anything approaching its former range and abundance will clearly require limiting the effects of deer browsing.

Although never as common as hemlock, northern white cedar is also a slow-growing, long-lived conifer sensitive to deer browsing that provides cover for deer yards in severe winters (Christensen 1954; Curtis 1959; Doepker and Ozoga 1990). White cedar, however, dominates particular sites such as limestone outcrops and lowland swamps (Habeck 1958; Curtis 1959), providing habitat for rare species, including orchids such as calypso orchid *Calypso bulbosa*, showy lady's-slipper *Cypripedium reginae*, large round-leaved orchid *Platanthera orbiculata*, and ram's head lady's-slipper *Cypripedium arietinum* (Epstein et al. 1999). Like hemlock, white cedar is failing to regenerate in most of the Great Lakes region, a situation attributed to deer browsing (Heitzman et al. 1997; Epstein et al. 1999; Van Deelen 1999). Because white cedar is both slow-growing and a favoured browse species in the winter, white cedar may be particularly vulnerable to deer (Aldous 1941; Beals et al. 1960; Rogers et al. 1981). Even on productive sites, it takes >20 years for white cedar to grow tall enough to avoid deer damage (Verme and Johnston 1986; Heitzman et al. 1997), yet experiments indicate that removing as little as 20% of their foliage is fatal (Aldous 1952). In examining the demography of northern white cedar populations at 77 lowland sites in the Great Lake States, we found patterns similar to those in hemlock, but with even more marked effects of deer browsing (Fig. 2b; Rooney et al. 2002). Thus, efforts to regenerate cedar swamps will also require either reductions in deer density or special efforts to mechanically protect saplings.

In an island study in Lake Superior, we found that Canada yew, mountain maple *Acer spicatum*, yellow birch *Betula allegheniensis*, and mountain ash (*Sorbus* ssp.) all decreased in response to increased deer density (Balgooyen and Waller 1995). Deer also restrict the regeneration of several other trees, including white pine *Pinus strobus* in Minnesota (Sauerman 1992), yellow and black birch *Betula lenta* in Pennsylvania (Horsley and Marquis 1983), and several species of oak (Strole and Anderson 1992; Robertson and Robertson 1995; Boerner and Brinkman 1996; Buckley et al. 1998; Ritchie et al. 1998). In addition to these direct effects of browsing, deer also exert indirect effects by favouring grasses and ferns that can interfere with tree seedling recruitment (Horsley and Marquis 1983; Stewart and Burrows 1989). Thus, demographic, island, and exclosure studies all demonstrate that high densities of deer reduce the ability of many woody plants to regenerate and that such effects are occurring across a wide region (McShea and Rappole 1992; Waller and Alverson 1997; Rooney et al. 2001).

3.4 Deer impacts on forest understory plants

Many herbaceous species are also sensitive to herbivory by deer and may decline markedly in abundance at high deer densities. However, evidence for these impacts is scarce, as herb species can disappear from a site and leave no trace. Without a demographic record at a site, it is difficult to infer their former abundance without historical or comparative studies. Nevertheless, assessing such effects is important, because most of the plant diversity in North American forests exists among the herbaceous species in forest understories. Herbs provide the bulk of late spring and summer forage for deer (McCaffery et al. 1974), which forage on them selectively, having greater effects on some species than others and thus acting to shift the composition of plant communities. In general, deer avoid grasses, sedges, and many ferns, preferring to feed on dicots, lilies, and orchids.

Miller et al. (1992) found no reports of deer impacts on rare graminoids, but deer posed a significant threat for a third or more of other rare plants. Studies in Minnesota forests also reveal that deer clearly prefer lilies like *Trillium* and *Uvularia*, even when they become rare (Augustine 1997). Large-flowered trillium *Trillium grandiflorum* in Illinois decline greatly in both height and number once deer exceed a density of 4–6/km^2 (Anderson 1994, 1997). Although potentially a long-lived species, surviving *Trillium* plants decrease in size and ability to flower once defoliated (Rooney and Waller 2001). In a comparative island study, we found that higher deer densities reduce the abundance of bluebead lily *Clintonia borealis*, wild sarsaparilla *Aralia nudicaulis*, and Canada mayflower *Maianthemum canadense* (Balgooyen and Waller 1995). Like large-flowered trillium, bluebead lily has an erect flower stalk that may be especially attractive to deer. In both species, deer nip flower and fruit stalks or diminish plant size to below the threshold needed for flowering, effectively eliminating reproduction even before vegetative plants have been grazed to oblivion. Deer similarly eliminate reproduction in yew by browsing the outer shell of foliage and male cones (Allison 1990a,b). In all these cases, deer above a threshold density of about 5 deer/km^2 appear to pose significant hazards for population persistence. In addition, we found that the impacts of high deer densities on herbs in the Apostle Islands persisted for more than 30 years, suggesting that restoration will take many decades.

In a study of herbs in the Allegheny region of Pennsylvania, Rooney (1997) found a lily (Canada mayflower) growing at larger size and at three times higher density and flowering more frequently on top of tall boulders compared with nearby short boulders. Common wood sorrel *Oxalis montana* showed no such differences, demonstrating that deer selectively graze particular species. Using a historical survey, Rooney and Dress (1997) showed that two old-growth hemlock and hemlock–beech stands in this area lost most (59% and 80%) species of their ground flora between 1929 and 1995. They attributed many of these losses to direct and indirect effects of deer herbivory and advocated sharp reductions in deer density and/or fencing to protect the diversity of these stands. Drayton and Primack (1996) also

documented massive species loss in a park outside Boston but did not infer mechanisms.

We have recently been investigating patterns of community change and species loss among 62 forest stands in upper Wisconsin and Michigan using historical surveys of these same sites compiled by J. Curtis and colleagues (Curtis 1959). These communities, on average, have lost >15% of their native plant species, but parks lacking deer hunting have lost over half their original plant diversity (Rooney et al. 2004). Most rare species have declined, while most already common species increased in abundance, causing sites to become increasingly dominated by habitat generalists. Grasses (especially *Poa*), sedges (*Carex*), exotics, and some ferns (e.g., lady fern *Athyrium filix-femina*) increased in abundance, while most lilies and orchids declined, with two species of miterwort *Mitella* and the lily *Streptopus* declining 80% or more. These changes cause sites to become more similar to each other as they lose species in a process termed biotic "homogenization" (McKinney and Lockwood 1999). The patterns (which species are declining or increasing and where losses are greatest) implicate deer as a major cause of these community changes, as does the Apostle Islands study, which found plant species diversity to decline in direct response to past deer densities (Balgooyen and Waller 1995).

3.5 Deer impacts on species at other trophic levels

Deer have been labelled a "keystone" herbivore for affecting the abundance of many other species, including those at other trophic levels, and for altering overall community structure (McShea and Rappole 1992; Waller and Alverson 1997). Several workers have noted effects on bird species. For example, a wildlife preserve in southwestern Pennsylvania supporting high densities of deer, elk *Cervus elaphus*, and mouflon sheep *Ovis aries* lost three bird species (Casey and Hein 1983). In another location in Pennsylvania, deCalesta (1994) noted marked declines in mid-canopy nesting birds at densities of 15 and 25 deer/km^2 as well as effects on small mammals. In studying the effects of silvicultural treatments, Brooks and Healy (1989) found that white-tailed deer had greater effect on small mammal abundances than did the treatments. McShea and Rappole (1997) also noted marked shifts in bird community structure in experimental deer enclosures, but these were sometimes the unexpected result of complex interactions with squirrels and acorn crops. Ostfeld et al. (1996) also noted complex interactions involving deer, squirrels, acorns, mice, and gypsy moths. These studies make clear how difficult it is to predict effects of high deer densities without detailed field data and a good understanding of biotic interactions.

Deer may also be influencing the dynamics of invading species. As noted above, deer herbivory tends to favour grasses and sedges, several of which are exotic species in Wisconsin (unpubl. data). By ingesting and dispersing seeds, deer could also be enhancing invasions of garlic mustard *Alliaria petiolata* or weedy shrubs like buckthorn *Rhamnus cathartica* or Asian honeysuckles (*Lonicera* spp.). Most regions north of the line of glacial advance have lacked native earthworms until recently, when European species invaded the region (Marinissen and van den Bosch 1992; C. Hale, pers. commun.). We have noted that sites suffering both earthworm invasion and high deer density experience disproportionately high losses in plant species diversity (S. Wiegmann, unpubl. data).

Deer may also influence other species by acting as a reservoir for parasites or pathogens. Efforts to reintroduce elk and moose in the Great Lake States encounter difficulties because deer harbour, as a nonlethal heartworm, a parasite that can act as a lethal brain worm *Parelaphostrongylus tenuis* in these other ungulates (Michigan Department of Natural Resources 2005). Deer can also affect the incidence of Lyme disease by supporting high populations of the spirochete's vector, deer ticks (Wilson et al. 1985, 1988, 1990; Deblinger et al. 1993; Van Buskirk and Ostfeld 1995). Massachusetts, Long Island, New York, and parts of the upper Midwest are all experiencing increases in the incidence of Lyme disease at a time of record deer densities.

More recently, outbreaks of bovine tuberculosis in Michigan and chronic wasting disease (CWD) in Wisconsin have been linked to high deer densities, deer feeding, and associated opportunities for disease transmission. Bovine tuberculosis poses a distinct risk to farmers in the region, leading to bans on feeding. CWD is a new transmissible spongiform encephalopathy disease similar to "mad cow" disease that may have been imported to Wisconsin from Colorado or Montana via game farm animals. In 2002, the Wisconsin Department of Natural Resources took the unprecedented action of declaring a "kill zone" to eradicate all deer from the focus of CWD infection, but hunting success has fallen short of what was hoped for because of both opposition by some private property owners and reduced hunting levels attributable to concerns over the risk that CWD meat may pose to human health. In addition, the CWD "kill zone" is limited to a small region, but cases have already appeared beyond this zone. If high deer densities have facilitated, or exacerbated, all these epidemics, we have a strong epidemiological, as well as an ecological, rationale for reducing deer densities.

In summary, deer sustained at high densities are acting as a keystone herbivore to greatly alter community dynamics in most forest stands across the eastern and central United States. It was initially argued that these effects were local, temporary, and restricted to a few sensitive species. This can no longer be claimed. Deer have significant impacts on many species across broad regions that have affected patterns of forest succession, composition, and diversity. These impacts may be difficult, or even impossible, to reverse. Despite research to date, our understanding of the number and magnitude of these effects is still incomplete, while our knowledge of how best to restore ecosystems degraded by overabundant deer is quite limited.

4. Opportunities and constraints in deer management

4.1 Conservation in whole or in part?

How will wildlife and forest managers respond to the many problems posed by hyperabundant deer? To date, responses have been local, proximal, and piecemeal.

Foresters faced with browsed seedlings move to fencing, "deer tubes," and repellants. Arboreta and natural area managers also fence rare plants and communities at high cost. Suburban landowners are hiring professional sharpshooters. Some communities have experimented with deer contraception and sterilization, but these have yet to prove cost-effective. Efforts to translocate animals result in high mortality and ignore region-wide deer overabundance. Farmers are issued special hunting permits as they document crop damage. Car insurance rates simply increase to accommodate the rising numbers of vehicle–deer accidents. These efforts each make sense in their limited context, but do little to address the broader issues of how to bring deer numbers back into balance with their habitat and long-evolved relationships with other species.

The review above makes clear that deer act as "ecosystem engineers" to restructure forests, change patterns of succession, and substantially alter the relative abundances of trees, shrubs, herbs, and possibly invading exotic species. Collectively, these results show that deer are simplifying the diversity of many forest ecosystems and homogenizing forest stands. Given that deer have widespread, profound, and long-lasting impacts on forest communities, these findings imply that managers are not managing just deer or deer habitat but rather whole ecosystems. They should therefore redefine their constituency as the general public and their domain of concern as the system (deCalesta and Stout 1997). By focusing less on the immediate interests of hunters and deer and more on the longer-term sustainability of the system, both deer and forests will ultimately benefit. Aldo Leopold argued persuasively for such wider concerns almost 60 years ago in his 1944 draft essay "Conservation: In whole or in part?" (Meine 1988: 464).

4.2 Can hunting regulate deer numbers?

In the early 20th century, limiting hunting to short seasons, restricting bag limits, favouring bucks over does, and enhancing deer habitat conditions all made sense. We must now rethink these conventional assumptions and practices and contemplate new approaches better able to limit deer numbers and impacts. In particular, which of the factors contributing to high deer densities (Table 1) can be modified so as to ratchet down deer densities?

In the short term, it seems most practical to increase hunter effort and/or efficiency. Longer seasons, larger bag limits, and antlerless hunts could expand the harvest in ways that could reduce population growth. The efficiency of hunting as a tool to control deer densities obviously hinges on hunter effort, particularly in reducing the number of reproductive does. Native Americans and others engaged in subsistence hunting often act effectively to limit deer densities by hunting over longer seasons and by taking both sexes. Requiring recreational hunters to shoot one or more antlerless animals before they are allowed to take a buck could also help to ensure that hunter effort is allocated in a way that achieves deer herd reductions. However, such shifts in culture may not come easily. In the late 1990s, when the Wisconsin Department of Natural Resources attempted to extend the 9-day gun season and introduce such an "Earn-a-buck" program, both proposals met with strong resistance from hunters who considered these changes improper deviations from time-honoured traditions. "Quality deer management" programs that emphasize the need to reduce antlerless deer numbers to support the growth of fewer, larger bucks appear somewhat more popular with hunters. While such approaches can bring reductions in density, managers should view them as an experimental tool, perhaps most valuable for educating hunters about a wider set of ecological values.

Table 1
Factors contributing, currently or historically, to high deer densities in eastern, southern, and central North America

Contributing factors	Examples
Favourable habitat conditions	Abundant early successional habitat
	Plentiful clearings
	Patchy distribution of habitats and many edge habitats
	Conifer stands to provide thermal cover and "yards" in winter[a]
Plentiful forage resources	High aspen (*Populus*) abundance
	Many forest openings
	Frequently available logging tops
	Supplemental feeding[a]
Mild winters[a]	The 1990s were the warmest decade on record
Low predation	Native predators (cougar, wolf) scarce
	Strict controls on human hunting (e.g., 9-day gun season; bucks favoured)
	Declines in hunter numbers or effort in many areas

[a] Particularly relevant along the northern edge of deer range.

While hunting is an obvious tool for controlling deer numbers, it may be unable to reduce deer densities in some years and locales. Hunting will succeed in limiting deer densities only if hunting efficacy increases sufficiently when deer numbers climb. If hunters fail to take an increasing proportion of deer as deer densities increase, their efforts will not act as a density-dependent control. In prey–predator systems, an outbreak of the prey population can surpass the predator's functional and numerical responses and thus their ability to regulate prey populations. Deer may already be beyond this "break-point" in regions where hunter numbers are low or hunting access is restricted. In such situations, hunting must be expanded or other density-dependent factors must come into play if we are to control deer densities. However, many hunters are reluctant to hunt does or take more than one or two animals. Thus, even if bag limits are expanded and hunting regulations focus the hunt on antlerless animals, there may not be enough willing hunters. With an increasingly urban populace, hunter numbers are also declining, while a vocal minority expresses strong antihunting sentiments. Hunters are also reluctant to hunt animals potentially contaminated with diseases like CWD or tuberculosis, reducing hunter effort just at a time of maximal need. Finally, hunter efforts are also limited by hunter access to private lands. As more private landowners post their lands against hunting, deer enjoy more refuges, and regional kill rates decline. Landowners restrict access for a variety of reasons, but might be persuaded to encourage more hunting

by some combination of public education, the right to regulate access, and tax incentives.

Managers should also reconsider how to define "carrying capacity" (MacNab 1985). Game managers have typically defined it with reference only to how many deer a given area could support, yet such numbers of deer are not generally compatible with the long-term persistence of all other species. The relative deer density that sustains the diversity of the system will almost always be lower, possibly far lower, than densities aimed at maximizing the yield of hunted deer (deCalesta and Stout 1997).

4.3 Other means to reduce deer densities

What other options exist for reducing deer numbers? Let us first consider the two ends of the wildness spectrum where human hunters are less effective. In urban and suburban areas, human population densities and civil regulations sharply restrict hunting. Sharpshooters can be effective in such areas, but communities must agree on the need and be willing to pay (DeNicola et al. 1997). At the other extreme, remote regions lacking road access attract few hunters. In such unmanaged landscapes, however, deer overpopulation tends to be less of a problem, as food resources are usually lower in unmanaged landscapes and wild predators may be present. Whether wild predators control ungulate populations has been a contentious issue in ecology, with some questioning A. Leopold's assertion that "a mountain lives in fear of losing its wolves" (Caughley 1970). Recent studies of cougar and wolf in Glacier National Park indicate that these predators can act as primary factors to control deer and elk populations (Kunkel and Pletscher 1999). Estimates of deer densities and impacts also appear lower within wolf pack territories in the Great Lake States region (unpubl. data). Even where predators do not control deer densities, they could modify deer aggregation or movements in a way that reduced their impacts (Brown et al. 1999). Such results suggest that reintroducing or restoring predators is a logical part of comprehensive programs to control overabundant deer.

In addition to controlling deer densities by "top-down" methods involving hunting or predators, it may also prove possible to reduce deer densities and impacts by "bottom-up" methods that limit the food resources available to deer. An obvious first step is to curtail the recreational feeding of deer that has increased so greatly in recent years. Supplemental deer feeding, along with intentional logging to provide additional woody browse in winter, seems likely to increase rates of overwinter survival and reproduction, although few quantitative studies exist. Both Michigan and Wisconsin have moved aggressively to ban deer feeding in recent years, but only in response to the epidemics mentioned above, and only in that part of Michigan with bovine tuberculosis. The ban on baiting deer to restrict nose-to-nose disease transmission could also lower hunter success.

It is also worth exploring how changes in forest and landscape management might contribute to reductions in deer density. Current "working forest" landscapes are managed more or less intensively, favouring early successional stands dominated by species like aspen. Logging "tops" provide plentiful browse, while the openings and edge habitats created by logging usually produce abundant summer forage. If "the way to manage game is to manage habitat" (Leopold 1933), perhaps habitat management could be run in reverse to regenerate the more mature, closed canopy, unfragmented habitat and landscape conditions that prevailed before European settlement. At least, intensive efforts to generate and maintain "wildlife openings" should be abandoned and replaced with experiments to evaluate the potential of such an approach. Given the mobility and movement patterns of deer, such programs would need to be large, encompassing 20 000 ha or more to be effective (an estimate based on average deer movements of 8 km). Areas of mature forest smaller than 8000 ha (e.g., the Sylvania Wilderness in Michigan's Upper Peninsula) appear insufficient to achieve this effect.

Forest and wildlife managers should take a more coordinated approach to managing forest ecosystems. The lowest deer densities and impacts in Wisconsin occur on Native American reservations, demonstrating the wisdom of combining liberal hunting regulations with less intensive forest management and more continuous canopy cover. The best long-term chance for reducing damaging deer impacts may be to combine less intensive methods of forest management with enhanced hunting and expanded populations of native predators. Such integrated solutions might also prove popular with the public, particularly if they are supported by effective education campaigns and strong research and monitoring programs.

4.4 Roles for research and monitoring

As wildlife and forest managers seek to address the manifold issues posed by hyperabundant deer, they will also need to rely more regularly and closely on research and monitoring to provide accurate information and informed models of how deer and habitats will respond to each other. While it may seem self-serving for a scientist to end a review of deer impacts with a call for more research, the facts presented should make clear that our understanding of deer–forest interactions remains far from complete. Managers committed to sustaining ecosystem diversity need research to determine the threshold densities at which deer have substantial impacts on particular species and how these impacts depend on the local abundances and mix of species. They are also keen to learn the deer densities compatible with sustaining overall species numbers and natural processes and how these thresholds vary across various species and landscapes. We also have much to learn about how temporal and spatial variations in deer densities affect their long-term impacts on natural systems. Can a few years of reduced deer densities once every few decades provide a "window" through which cohorts of tree seedlings can grow enough to ensure successful regeneration?

Managers must also seek a clearer picture of the complex and long-lasting ways in which deer modify forest ecosystems. Once plant communities are simplified and homogenized by an excess of deer, they may be quite slow to recover their original diversity and patterns of abundance. Many forest herbs are long-lived and slow-growing, with limited dispersal capability, making them slow to recolonize sites. In addition, deer affect plant species differently at

different densities, having greater proportional impacts once species become rare (Augustine and Frelich 1998; Augustine et al. 1998). This could significantly delay or even prevent recovery of plant populations once they are reduced in abundance, resulting in an "alternative stable state." Such ecological "hysteresis" (the inability of a system to return to a state by the same path that it came to that state) may typify plant communities simplified by deer. We thus need more research both to characterize how plant communities decay in response to overabundant deer and to understand the dynamics of how communities recover once deer densities and impacts are reduced.

Managers would also clearly benefit from better monitoring of deer impacts. No pilot would be expected to fly a modern airplane without accurate indicators of location, speed, direction, etc. Resource managers work with systems that are at least as complex and less predictable. They deserve ready access to detailed field data regarding deer numbers and impacts and models of the likely effects of deer impacts at such densities on species interactions. They particularly need reliable and efficient (inexpensive) indicators capable of serving as "early warning signals" of impending community degradation (and recovery). Research will be needed to develop and test these indicators, but such work could be coordinated regionally to share resources. It seems logical to devote some reasonable fraction of licensing or operating budget revenues to such work as the routine "cost of doing business" (Waller and Alverson 1997). Once effective monitoring methods are developed, it may be possible to involve volunteer teachers, naturalists, and others to create "citizen science" monitoring networks efficiently connected to researchers and managers via web-based geographical databases. We are currently involved in establishing such a program in Wisconsin.

Finally, as managers seek to stay abreast of the information now accumulating regarding deer impacts, they should also be alert to opportunities to integrate management more fully with research and monitoring. The ideal of *adaptive management*—closely integrating research and monitoring with management activities so that each informs the other—has existed for decades (Holling 1978; Walters 1986). Nevertheless, resource managers would benefit by implementing this paradigm more fully (Holling and Meffe 1996; Nielsen et al. 1997).

Acknowledgements

Many collaborators helped to conduct the studies reviewed here. W. Alverson, S. Solheim, and E. Judziewicz first stimulated my interest in deer impacts, while T. Rooney, S. Wiegmann, and D. Rogers have done much of the recent work. I am grateful for their efforts and insights. T. Rooney also provided comments on the manuscript and helped me to find references. J.-L. Martin and A.J. Gaston provided encouragement, stimulating discussions, and the special opportunity of participating in the Haida Gwaii conference.

Literature cited

Aldous, S.E. 1941. Deer management suggestions for northern white cedar types. J. Wildl. Manage. 5: 90–94.

Aldous, S.E. 1952. Deer browse clipping study in the Lakes States region. J. Wildl. Manage. 16: 401–409.

Allen, S.W.; Sharpe, G.W. 1960. An introduction to American forestry. McGraw-Hill Book Co., New York.

Allison, T.D. 1990a. The influence of deer browsing on the reproductive biology of Canada yew (*Taxus canadensis* Marsh.). I. Direct effect on pollen, ovule, and seed production. Oecologia 83: 523–529.

Allison, T.D. 1990b. The influence of deer browsing on the reproductive biology of Canada yew (*Taxus canadensis* Marsh.). II. Pollen limitation: an indirect effect. Oecologia 83: 530–534.

Alverson, W.S.; Waller, D.M. 1997. Deer populations and the widespread failure of hemlock regeneration in northern forests. Pages 280–297 *in* W.J. McShea, H.B. Underwood, and J.H. Rappole (eds.), The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C.

Alverson, W.S.; Waller, D.M.; Solheim, S.L. 1988. Forests too deer: Edge effects in northern Wisconsin. Conserv. Biol. 2: 348–358.

Alverson, W.S.; Kuhlmann, W.; Waller, D.M. 1994. Wild forests: conservation biology and public policy. Island Press, Washington, D.C.

Anderson, R.C. 1994. Height of white-flowered trillium (*Trillium grandiflorum*) as an index of deer browsing intensity. Ecol. Appl. 4: 104–109.

Anderson, R.C. 1997. Native pests: the impact of deer in highly fragmented landscapes. Pages 117–134 *in* M.W. Schwartz (ed.), Conservation in highly fragmented landscapes. Chapman & Hall, New York.

Anderson, R.C.; Katz, A.J. 1993. Recovery of browse-sensitive tree species following release from white-tailed deer (*Odocoileus virginianus* Zimmerman) browsing pressure. Biol. Conserv. 63: 203–208.

Anderson, R.C.; Loucks, O.L. 1979. White-tailed deer (*Odocoileus virginianus*) influence on the structure and composition of *Tsuga canadensis* forests. J. Appl. Ecol. 16: 855–861.

Augustine, D.J. 1997. Grazing patterns and impacts of white-tailed deer in a fragmented forest ecosystem. University of Minnesota, St. Paul, Minnesota.

Augustine, D.J.; Frelich, L.E. 1998. White-tailed deer impacts on populations of an understory forb in fragmented deciduous forests. Conserv. Biol. 12: 995–1004.

Augustine, D.J.; Frelich, L.E.; Jordan, P.A. 1998. Evidence for two alternative stable states in an ungulate grazing system. Ecol. Appl. 8: 1260–1269.

Balgooyen, C.P.; Waller, D.M. 1995. The use of *Clintonia borealis* and other indicators to gauge impacts of white-tailed deer on plant communities in northern Wisconsin, USA. Nat. Areas J. 15: 308–318.

Beals, E.W.; Cottam, G.; Vogel, R.G. 1960. Influence of deer on the vegetation of the Apostle Islands, Wisconsin. J. Wildl. Manage. 24: 68–80.

Blewett, T.J. 1976. Structure and dynamics of the McDougall Springs lowland forest. Department of Botany, University of Wisconsin, Madison, Wisconsin. 86 pp.

Boerner, R.E.J.; Brinkman, J.A. 1996. Ten years of tree seedling establishment and mortality in an Ohio deciduous forest complex. Bull. Torrey Bot. Club 123: 309–317.

Braun, E.L. 1950. Deciduous forests of eastern North America. Blakiston Company, Philadelphia, Pennsylvania.

Brooks, R.T.; Healy, W.M. 1989. Response of small mammal communities to silvicultural treatments in eastern hardwood forests of West Virginia and Massachusetts. Pages 313–318 *in* Management of amphibians, reptiles, and small mammals in North America. Forest Service, U.S. Department of Agriculture, Washington, D.C.

Brown, J.S.; Laundré, J.W.; Gurung, M. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. J. Mammal. 80: 385–399.

Buckley, D.S.; Sharik, T.L.; Isebrands, J.G. 1998. Regeneration of northern red oak: positive and negative effects of competitor removal. Ecology 79: 65–78.

Casey, D.; Hein, D. 1983. Effects of heavy browsing on a bird community in a deciduous forest. J. Wildl. Manage. 47: 829–836.

Caughley, G. 1970. Eruption of ungulate populations, with special emphasis on Himalayan Thar of New Zealand. Ecology 51: 3–72.

Christensen, E.M. 1954. A phytosociological study of the winter range of deer of northern Wisconsin. University of Wisconsin, Madison, Wisconsin.

Clark, J.S.; Beckage, B.; Camill, P.; Cleveland, B.; HilleRisLambers, J.; Lichter, J.; McLachlan, J.; Mohan, J.; Wyckoff, P. 1999. Interpreting recruitment limitation in forests. Am. J. Bot. 86: 1–16.

Cronon, W. 1983. Changes in the land: Indians, colonists, and the ecology of New England. Hill and Wang, New York.

Curtis, J.T. 1959. The vegetation of Wisconsin. University of Wisconsin Press, Madison, Wisconsin.

Davis, M.B. 1987. Invasions of forest communities during the Holocene: beech and hemlock in the Great Lakes region. Pages 373–393 *in* A.J. Gray, M.J. Crawley, and P.J. Edwards (eds.), Colonization, succession, and stability. Blackwell Scientific, Oxford, U.K.

Deblinger, R.D.; Wilson, M.L.; Rimmer, D.W.; Spielman, A. 1993. Reduced abundance of immature *Ixodes dammini* (Acari: Ixodidae) following incremental removal of deer. J. Med. Entomol. 30: 144–150.

deCalesta, D.S. 1994. Effect of white-tailed deer on songbirds within managed forests in Pennsylvania. J. Wildl. Manage. 58: 711–717.

deCalesta, D.S.; Stout, S.L. 1997. Relative deer density and sustainability: a conceptual framework for integrating deer management with ecosystem management. Wildl. Soc. Bull. 25: 252–258.

DeNicola, A.J.; Weber, S.J.; Bridges, C.A.; Stokes, J.L. 1997. Nontraditional techniques for management of overabundant deer populations. Wildl. Soc. Bull. 25: 496–499.

Doenier, P.B.; DelGiudice, G.D.; Riggs, M.R. 1997. Effects of winter supplemental feeding on browse consumption by white-tailed deer. Wildl. Soc. Bull. 25: 235–243.

Doepker, R.V.; Ozoga, J.J. 1990. Wildlife values of northern white-cedar. Pages 15–34 *in* D.O. Lantagne (ed.), Proceedings of the northern white cedar in Michigan workshop. Michigan State University Agricultural Experiment Station Research Report 512, Michigan State University, East Lansing, Michigan.

Drayton, B.; Primack, R.B. 1996. Plant species lost in an isolated conservation area in metropolitan Boston from 1894 to 1993. Conserv. Biol. 10: 30–39.

Eckstein, R.G. 1980. Eastern hemlock (*Tsuga canadensis*) in north central Wisconsin. Wisconsin Department of Natural Resources, Madison, Wisconsin.

Epstein, E.; Smith, W.; Dobberpuhl, J.; Galvin, A. 1999. Biotic inventory and analysis of the Brule River State Forest. Bureau of Endangered Resources, Wisconsin Department of Natural Resources, Madison, Wisconsin.

Fox, S.R. 1981. The American conservation movement: John Muir and his legacy. University of Wisconsin Press, Madison, Wisconsin.

Frelich, L.E.; Lorimer, C.G. 1985. Current and predicted long-term effects of deer browsing in hemlock forests in Michigan, U.S.A. Biol. Conserv. 34: 99–120.

Frelich, L.E.; Reich, P.B. 1995. Neighborhood effects, disturbance, and succession in forests of the western Great Lakes region. Ecoscience 2: 148–158.

Frelich, L.E.; Calcote, R.R.; Davis, M.B.; Pastor, J. 1993. Patch formation and maintenance in an old-growth hemlock–hardwood forest. Ecology 74: 513–527.

Garrott, R.A.; White, P.J.; White, C.A.V. 1993. Overabundance: an issue for conservation biologists? Conserv. Biol. 7: 944–949.

Gill, R.M.A. 1992. A review of damage by mammals in north temperate forests: 1. Deer. Forestry 65: 145–169.

Graham, S.A. 1958. Results of deer exclosure experiments in the Ottawa National Forest. Trans. N. Am. Wildl. Conf. 23: 478–490.

Habeck, J.R. 1958. White cedar ecotypes in Wisconsin. Ecology 39: 457–463.

Hadidian, J. 1993. Science and management of white-tailed deer in the U.S. National Parks. Pages 77–85 *in* W.E. Brown and J.S.D. Veirs (eds.), Partners in stewardship: Proceedings of the 7th conference on research and resource management in parks and on public lands. George Wright Society, Hancock, Michigan.

Harlow, R.F.; Downing, R.L. 1970. Deer browsing and hardwood regeneration in the southern Appalachians. J. For. 68: 298–300.

Healy, W.M. 1971. Forage preferences of tame deer in a northwest Pennsylvania clearcutting. J. Wildl. Manage. 35: 717–723.

Heitzman, E.; Pregitzer, K.S.; Miller, R.O. 1997. Origin and development of northern white-cedar stands in northern Michigan. Can. J. For. Res. 27: 1953–1961.

Holling, C.S. 1978. Adaptive environmental assessment and management. John Wiley & Sons, New York. 377 pp.

Holling, C.S.; Meffe, G.K. 1996. Command and control and the pathology of natural resource management. Conserv. Biol. 10: 328–337.

Horsley, S.B.; Marquis, D.A. 1983. Interference by weeds and deer with Allegheny hardwood reproduction. Can. J. For. Res. 13: 61–69.

Hough, A.F. 1965. A twenty-year record of understory vegetational change in a virgin Pennsylvania forest. Ecology 46: 370–373.

Kroll, J.C.; Goodrum, W.D.; Behrman, P.J. 1988. Twenty seven years of over-browsing: Implications to white-tailed deer management on wilderness areas. Pages 294–303 *in* D.L. Kulhavy and R.N. Conner (eds.), Wilderness and natural areas in the eastern United States: A management challenge. School of Forestry, Stephen F. Austin State University, Nacogdoches, Texas.

Kunkel, K.; Pletscher, D.H. 1999. Species-specific population dynamics of cervids in a multi-predator system. J. Wildl. Manage. 63: 1082–1093.

Leopold, A. 1933. Game management. Charles Scribner's Sons, New York.

Leopold, A. 1936. Deer and Dauerwald in Germany. I. History. J. For. 34: 366–375.

Leopold, A. 1943. The excess deer problem. Audubon 45: 156–157.

Leopold, A. 1946. The deer dilemma. Wisc. Conserv. Bull. 11: 3–5.

Leopold, A.; Sowls, K.; Spencer, D.L. 1947. A survey of over-populated deer ranges in the U.S. J. Wildl. Manage. 11: 162–177.

Lutz, H.J. 1930. Effect of cattle grazing on vegetation of a virgin forest in northwestern Pennsylvania. J. Agric. Res. 41: 561–570.

MacNab, J. 1985. Carrying capacity and related slippery shibboleths. Wildl. Soc. Bull. 13: 403–410.

Marinissen, J.C.Y.; van den Bosch, F. 1992. Colonization of new habitats by earthworms. Oecologia 91: 371–376.

Marquis, D.A. 1974. The impact of deer browsing on Allegheny hardwood regeneration. Report No. NE 57, Northeast Forest Experiment Station, Forest Service, U.S. Department of Agriculture, Warren, Pennsylvania.

Marquis, D.A. 1975. The Allegheny hardwood forests of Pennsylvania. General Technical Report No. NE 15, Northeastern Research Station, Forest Service, U.S. Department of Agriculture. 32 pp.

Marquis, D.A. 1981. Effect of deer browsing on timber in Allegheny hardwood forests of northwestern Pennsylvania. Report No. NE 47, Northeast Forest Experiment Station, Forest Service, U.S. Department of Agriculture, Warren, Pennsylvania.

Martin, J.-L.; Baltzinger, C. 2002. Interaction among deer browsing, hunting, and tree regeneration. Can. J. For. Res. 32: 1254–1264.

McCabe, R.E.; McCabe, T.R. 1984. Of slings and arrows: An historical retrospective. Pages 19–72 *in* L.K. Halls (ed.), White-tailed deer ecology and management. Stackpole Books, Harrisburg, Pennsylvania.

McCaffery, K. 1986. On deer carrying capacity in northern Wisconsin. Pages 54–69 *in* Proceedings of the 22nd Northeast Deer Technical Committee. Vermont Fish and Wildlife Department, Waterbury, Vermont.

McCaffery, K.R.; Tranetzki, J.; Piechura, J. 1974. Summer foods of deer in northern Wisconsin. J. Wildl. Manage. 38: 215–219.

McCullough, D.R. 1984. Lessons from the George Reserve, Michigan. Pages 211–242 *in* L.K. Halls (ed.), White-tailed deer ecology and management. Stackpole Books, Harrisburg, Pennsylvania.

McKinney, M.L.; Lockwood, J.L. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol. Evol. 14: 450–453.

McShea, W.J.; Rappole, J.H. 1992. White-tailed deer as keystone species within forested habitats of Virginia. Va. J. Sci. 43: 177–186.

McShea, W.J.; Rappole, J.H. 1997. Herbivores and the ecology of forest understory birds. Pages 298–309 *in* W.J. McShea, H.B. Underwood, and J.H. Rappole (eds.), The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C.

McShea, W.J.; Underwood, H.B.; Rappole, J.H. (eds.). 1997. The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C.

Meine, C. 1988. Aldo Leopold: His life and work. University of Wisconsin Press, Madison, Wisconsin.

Michigan Department of Natural Resources. 2005. Brainworm web site: http://www.michigan.gov/dnr/1,1607,7-153-10370_12150_12220-26502--,00.html.

Miller, S.G.; Bratton, S.P.; Hadidian, J. 1992. Impacts of white-tailed deer on endangered plants. Nat. Areas J. 12: 67–74.

Mladenoff, D.J.; Stearns, F. 1993. Eastern hemlock regeneration and deer browsing in the northern Great Lakes region: A re-examination and model simulation. Conserv. Biol. 7: 889–900.

Nichols, G.E. 1935. The hemlock – white pine – northern hardwood region of eastern North America. Ecology 16: 403–422.

Nielsen, C.K.; Porter, W.F.; Underwood, H.B. 1997. An adaptive management approach to controlling suburban deer. Wildl. Soc. Bull. 25: 470–477.

Ostfeld, R.S.; Jones, C.G.; Wolff, J.O. 1996. Of mice and mast. BioScience 46: 323–330.

Ritchie, M.E.; Tilman, D.; Knops, J.M.H. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. Ecology 79: 165–177.

Robertson, D.J.; Robertson, M.C. 1995. Eastern mixed mesophytic forest restoration. Restor. Manage. Notes 13: 64–70.

Rogers, L.L.; Mooty, J.J.; Dawson, D. 1981. Foods of white-tailed deer in the Upper Great Lakes Region—a review. North Central Experiment Station, Forest Service, U.S. Department of Agriculture, St. Paul, Minnesota.

Rooney, T.P. 1997. Escaping herbivory: refuge effects on the morphology and shoot demography of the clonal forest herb, *Maianthemum canadense*. Bull. Torrey Bot. Club 124: 280–285.

Rooney, T.P. 2001. Impacts of white-tailed deer to forest ecosystems: a North American perspective. Forestry 74: 201–208.

Rooney, T.P.; Dress, W. 1997. Patterns of plant diversity in overbrowsed old growth and mature second growth hemlock–northern hardwood forest stands. J. Torrey Bot. Soc. 124: 43–51.

Rooney, T.P.; Waller, D.M. 1998. Local and regional variation in hemlock seedling establishment in forests of the upper Great Lakes region, USA. For. Ecol. Manage. 111: 211–224.

Rooney, T.P.; Waller, D.M. 2001. How experimental defoliation and leaf height affect growth and reproduction in *Trillium grandiflorum*. J. Torrey Bot. Soc. 128: 393–399.

Rooney, T.P.; Waller, D.M. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. For. Ecol. Manage. 181: 165–176.

Rooney, T.P.; McCormick, R.J.; Solheim, S.L.; Waller, D.M. 2000. Regional variation in recruitment of eastern hemlock seedlings in the Southern Superior Uplands Section of the Laurentian Mixed Forest Province, USA. Ecol. Appl. 10: 1119–1132.

Rooney, T.P.; Wiegmann, S.M.; Waller, D.M. 2001. Deer as a keystone herbivore: Implications for biological diversity in forest ecosystems. Forest Dynamics and Ungulate Herbivory, Davos, Switzerland.

Rooney, T.P.; Solheim, S.L.; Waller, D.M. 2002. Factors influencing the regeneration of northern white cedar in lowland forests of the Upper Great Lakes region, USA. For. Ecol. Manage. 163: 119–130.

Rooney, T.P.; Wiegmann, S.M.; Rogers, D.A.; Waller, D.M. 2004. Biotic impoverishment and homogenization in unfragmented forest understory communities. Conserv. Biol. 18: 787–798.

Ruhren, S.; Dudash, M. 1996. Consequences of the timing of seed release of *Erythronium americanum* (Liliaceae), a deciduous forest myrmecochore. Am. J. Bot. 83: 633–640.

Sauerman, K. 1992. Artificially established white pine plantations in Minnesota: a survey. Plan B Paper 74, University of Minnesota, Minneapolis, Minnesota.

Stewart, G.H.; Burrows, L.E. 1989. The impact of white-tailed deer *Odocoileus virginianus* on regeneration in the coastal forests of Stewart Island, New Zealand. Biol. Conserv. 49: 275–293.

Strole, T.A.; Anderson, R.C. 1992. White-tailed deer browsing: species preferences and implications for central Illinois forests. Nat. Areas J. 12: 139–144.

Tilghman, N.G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. J. Wildl. Manage. 53: 424–453.

Van Buskirk, J.; Ostfeld, R.S. 1995. Controlling Lyme disease by modifying the density and species composition of tick hosts. Ecol. Appl. 5: 1133–1140.

Van Deelen, T.R. 1999. Deer–cedar interactions during a period of mild winters: Implications for conservation of conifer swamp deeryards in the Great Lakes region. Nat. Areas J. 19: 263–274.

Verme, L.J.; Johnston, W.F. 1986. Regeneration of northern white cedar deeryards in Upper Michigan. J. Wildl. Manage. 50: 307–313.

Waller, D.M.; Alverson, W.S. 1997. The white-tailed deer: a keystone herbivore. Wildl. Soc. Bull. 25: 217–226.

Waller, D.M.; Alverson, W.S.; Solheim, S. 1996. Local and regional factors influencing the regeneration of eastern hemlock. Pages 73–90 *in* G. Mroz and J. Martin (eds.), Hemlock ecology and management: Proceedings of a regional conference on ecology and management of eastern hemlock. Department of Forestry, Michigan Technical University, Houghton, Michigan.

Walters, C.J. 1986. Adaptive management of renewable resources. MacMillan & Co., New York.

Warren, R.J. 1991. Ecological justification for controlling deer populations in eastern national parks. Trans. N. Am. Wildl. Nat. Resour. Conf. 56: 56–66.

Watson, A. 1983. Eighteenth century deer numbers and pine regeneration near Braemar, Scotland. Biol. Conserv. 25: 289–305.

Webb, W.L.; King, R.T.; Patric, E.F. 1956. Effect of white-tailed deer on a mature northern hardwood forest. J. For. 54: 391–398.

Williams, M. 1989. Americans and their forests: A historical geography. Cambridge University Press, New York.

Wilson, M.L.; Adler, G.H.; Spielman, A. 1985. Correlation between abundance of deer and that of the deer tick, *Ixodes dammini* (Acari: Ixodidae). Ann. Entomol. Soc. Am. 78: 172–176.

Wilson, M.L.; Telford, S.R.; Piesman, J.; Spielman, A. 1988. Reduced abundance of immature *Ixodes dammini* (Acari: Isodidae) following elimination of deer. J. Med. Entomol. 25: 224–228.

Wilson, M.L.; Ducey, A.M.; Litwin, T.S.; Gavin, T.A.; Spielman, A. 1990. Microgeographic distribution of immature *Ixodes dammini* ticks correlated with that of deer. Med. Vet. Entomol. 4: 151–159.

Zimmermann, G. 1995. The Atlantic white-cedar (*Chamaecyparis thyoides*) regeneration experiments: Final report. Richard Stockton College of New Jersey, New Brunswick, New Jersey.

Zimmermann, G. 2000. The Atlantic white cedar (*Chamaecyparis thyoides*) regeneration experiments: Final report. Richard Stockton College of New Jersey, New Jersey Department of Environmental Protection, New Brunswick, New Jersey. 105 pp.

White-tailed deer population reduction and control in four southwest Ontario protected heritage areas

Dan Reive and Bill Stephenson

Abstract

Overabundant white-tailed deer *Odocoileus virginianus* have become a significant management concern throughout northeastern North America. Because much of this area is heavily populated and intensively developed, simple hunting season adjustments are most often inappropriate tools to reduce herd numbers. The deer are found within the boundaries of cities, towns, suburbs, areas of intensive agriculture, and a range of parks and protected areas. The concerns of the people who live with high populations of deer must be considered and resolved.

Four protected heritage areas in southwest Ontario have undertaken white-tailed deer management to reduce, then maintain, the size of populations within their jurisdictions. These are Point Pelee National Park, Long Point National Wildlife Area, Rondeau Provincial Park, and Pinery Provincial Park. The first three areas are sandspit formations on the north shore of Lake Erie, the latter a forested dune complex on the shore of Lake Huron. Each is effectively an island of natural habitat in a densely settled and extensively modified landscape. All four parks needed to address a list of considerations that can be largely derived from scientific literature, now that deer population management has been widely undertaken across eastern North America. They are impacts of overpopulation on habitats, behaviour in relation to the regional deer herd, herd demographics, herd reduction and control options, implementation logistics, and communication strategies at various levels.

While the other three protected heritage areas worked through these considerations in slightly different ways than at Point Pelee National Park (which is highlighted here), all have successfully implemented, and made operational, white-tailed deer herd reduction and control programs.

1. Introduction

Overabundant white-tailed deer *Odocoileus virginianus* have become a significant management concern in northeastern North America. Deer populations have the potential for rapid growth in areas of excellent habitat. Adult does normally produce twin fawns and, rarely, triplets. Yearling does can produce twins, and fawns can be bred and give birth in their first year of life. In the absence of significant predation or hunting, this kind of reproduction can result in a deer herd doubling in size in 1 year (Ellingwood and Caturano 1988). For example, on the 646-ha George Reserve in southern Michigan, the deer herd grew from 6 to 162 individuals in 6 years (1928–1933) (McCullough 1979). More recently, the George Reserve herd grew from 10 deer in 1975 to 212 deer in 1980 (McCullough 1984). When the biological carrying capacity is exceeded, competition for limited food resources results in overbrowsing (Dasmann 1971, 1981). Severe overbrowsing alters plant species composition, distribution, and abundance and reduces understory structural diversity (due to the inability of seedlings to establish themselves). Deer overabundance often leads to a high frequency of deer–vehicle collisions, as well as extensive damage to commercial forests, agricultural crops, nursery stock, and landscape plantings (Marquis and Brennemann 1981; Matschke et al. 1984).

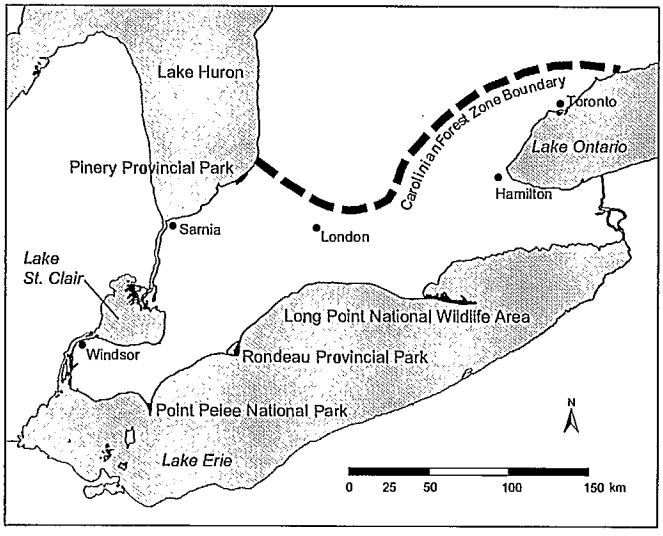
2. Study area

Southwestern Ontario comprises less than 1% of the country's land mass and is home to more than 25% of the country's human population. In colonial times, the Carolinian Forest Zone in southwestern Ontario was dominated by extensive tracts of mature hardwood forest. Early records suggest that deer were present in moderate numbers at the time. By the turn of the 20th century, deer populations were small and scattered primarily as a result of habitat loss due to extensive forest clearing for agriculture and unregulated hunting. As the human population expanded, creating a mosaic of small woodlots and cash crop agriculture among the towns and cities, and hunting became much more regulated and restricted, deer populations expanded. By the late 20th century, deer were found in towns, city suburbs, and areas of intensive agriculture and throughout a range of remnant parks and protected heritage areas (PHAs). The concerns of people and PHA land managers who live with overabundant deer herd situations must be considered and resolved. Effective herd management is necessary to meet ecological integrity and vegetation management targets as well as resolve land use practice and human safety and health concerns (Matschke et al. 1984; Ellingwood and Spignesi 1986; Canadian Parks Service 1990).

Four PHAs in southwestern Ontario have undertaken white-tailed deer management to reduce and then control the size of the deer populations within their jurisdictions. These are Point Pelee National Park (PPNP) (1565 ha), Long Point National Wildlife Area (LPNWA) (3250 ha), Rondeau Provincial Park (RPP) (3254 ha), and Pinery Provincial Park (PPP) (2100 ha) (Fig. 1). The first three areas are sandspit formations on the north shore of Lake Erie, the latter a forested dune complex on the east shore of Lake Huron. Each is effectively an island of natural habitat in a densely settled and extensively modified landscape.

PPNP, the primary focus of this paper, is a 15-km^2 peninsula extending south into the western basin of Lake Erie. The main ecosystem components are the 11-km^2 freshwater cattail *Typha* × *glauca* marsh and the 4-km^2 terrestrial habitat. The terrestrial components are predominately sand barrier beach, forested dunes, ridge and trough swamp forest, and open sand barrens with eastern red cedar *Juniperus virginiana* and oak (*Quercus* sp.) savannah characteristics. The Essex County Natural Heritage Features map (Fig. 2) clearly shows the biogeographic island effect—less than 6% of the surrounding landscape remains in natural habitat, and less than 2% of the original wetlands remain. Very little public land remains in natural cover; most woodlots are small and privately managed. PPNP was one of the first Canadian national parks established (in 1918) primarily for its biological value. Its unique southern flora and fauna, as well as its bird and insect migration phenomena, were instrumental in its early addition to the national park system. PPNP partially represents the southern "Carolinian Forest Zone" and has been home to over 60 species at risk designated by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2002).

Figure 1
Map of southwestern Ontario protected heritage areas



3. Management considerations

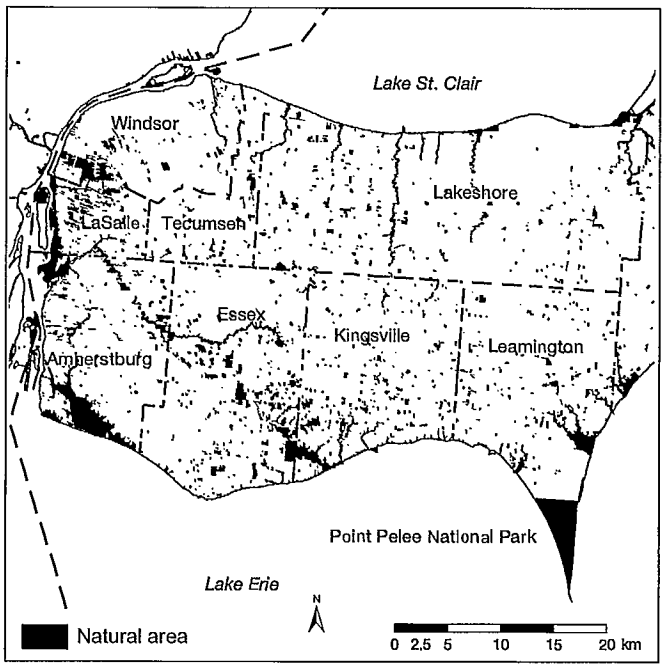
PPNP, along with the other three PHAs, needed to address a list of considerations that can be largely derived from scientific literature, now that deer population management has been widely undertaken across eastern North America. They are impacts of overpopulation on habitats, behaviour in relation to regional deer herds, herd demographics, herd reduction and vegetation management strategies, implementation logistics, and communication strategies.

3.1 Habitat impacts

PPNP is not a truly representative sample of the Carolinian Forest Zone (Parks Canada 1995). It has remnant components typical of early successional sandspits on Lake Erie. The park has been heavily impacted by human activities since its inception. Upwards of 400 cottages, houses, orchard and cash crop farms, and businesses once thrived inside park boundaries. In addition, visitation peaked at approximately 750 000 per year by the mid-1960s. The deer population throughout the 1950s was less than 10 animals; population estimates in the early 1970s were consistently under 30 animals. An aggressive private land acquisition program over the last 35 years has been recently completed. Most of the former private lands have been passively and/or actively restored, increasing the early successional habitats favoured by species such as white-tailed deer. With the reduction in park residents and improving habitat, the deer herd increased throughout the 1970s and 1980s.

By the late 1980s, staff noted significant impacts, such as increased vehicle collisions, proliferation of game trails, extensive browse lines on eastern red cedar trees, and increased complaints of deer feeding activities from

Figure 2
Map of Essex County natural heritage features



the cash crop (corn, radish, onion) farmers just north of the park boundary. It also became apparent from the scientific literature that overabundant deer herds had become a concern across much of their range. The other three PHAs in southern Ontario experienced similar growth in deer populations. LPNWA and RPP had a history of controlling deer populations as far back as the early 20th century, but by the late 1960s had largely abandoned the practice due to adverse public pressure.

By the late 1980s, Parks Canada staff initiated development of a Natural Resource Management Plan, concentrating on monitoring herd numbers, habitat use, movements, demographics, recruitment/mortality, winter severity, etc. (Hutchinson et al. 1988), with only a cursory review of deer herd control options. By the plan's completion, staff realized that the park was already past the need for extensive monitoring and decided to better document the impacts on vegetation communities in the park by way of fenced exclosures, forest regeneration plots (Mosquin 1988), and rare plant monitoring (Landplan Collaborative Ltd. 1990a).

3.2 Regional herd interaction

A radiotelemetry project began in 1987 in order to determine the home range size and seasonal movements of deer within the park. Bait stations and blinds were set up in various park habitats, and deer were darted using a variety of darting systems. Radio collars were installed on 18 deer and their movement patterns tracked for 12 months (Leggo 1989). The project data were also used to determine, during practical tests, the level of effort required to remotely dart females should the park eventually decide to use immunocontraception to reduce and maintain herd numbers. No meaningful interaction with the remnant deer population outside the park was found during the radio-tracking exercise. A few animals, predominately adult males whose normal activity area was in the cattail marsh near the north park boundary, did move out of the park on a daily basis to feed on agricultural crops, but essentially the park population was considered an isolated herd.

3.3 Herd demographics

During the same time frame as the telemetry project, deer drives were conducted by staff and volunteers on an annual basis, usually during early winter when snow cover was consistent and males still held their antlers. By providing training to volunteers, reasonably accurate data on total population, age structure, and sex ratio were obtained. Recruitment was determined by the ratio of does to young of the year, while mortality was estimated by the number of predated carcasses and road-killed animals located throughout the year. Review of the scientific literature indicated that a population of 6–8 deer/km^2 of available habitat results in little alteration of plant species abundance, composition, distribution, and understory structural diversity. Considering that PPNP has little more than 4 km^2 of terrestrial habitat, the carrying capacity of the park ranges from 24 to 32 animals. By the winter of 1990, ground counts indicated that the park herd had grown to over 160 animals. Allowing high deer densities over the long term will result in a highly degraded understory with low species diversity and poor regeneration of woody and herbaceous plants (McCullough and Robinson 1988).

3.4 Vegetation management strategies and herd reduction

Before selecting any deer management actions, the park formalized its Vegetation Management Goals and Objectives (Landplan Collaborative Ltd. 1990b) and ensured that the issue was recognized in the management plan (Parks Canada 1995). These provided both an ecological and policy context for decision-making.

Various vegetation protection and deer herd reduction strategies were considered for PPNP based on those identified by Ellingwood and Caturano (1988). An issue analysis exercise was completed for the park (Canadian Parks Service 1990) that assessed the pros and cons of various management techniques. They are summarized below:

1. *Do nothing/allow nature to take its course:* In the absence of effective, natural predator controls and the high reproductive capability of deer, significant impacts on vegetation community structure and composition would continue to occur. Reductions in forest breeding bird populations as well as extirpation of some rare plant species were forecasted to occur. Economic impacts on neighbouring farmers and deer–vehicle collisions would continue to rise. Park vegetation management objectives would not be met in the long term, and the park's goal of maintaining and enhancing ecological integrity would be compromised.
2. *Capture and relocation:* The tranquillization and transportation of large numbers of deer to release locations authorized by the provincial Ministry of Natural Resources were considered, as this option has been utilized in other areas of North America. There are high initial and ongoing logistical costs, lack of available underpopulated habitats, and high mortality rates associated with this option.
3. *Physical barriers and repellents:* Fencing has been used extensively by others for the protection of small site-specific areas primarily for agricultural purposes. Variations on implementation range from small fenced areas for short periods of time, permitting vegetation to recover, to permanent fencing to exclude deer. The technique of fencing areas within the park on a rotational basis would allow a patchwork of vegetation communities to recover and develop. Chemical repellents have been used in agricultural, urban, and arboretum-type settings where site-specific solutions have been required. Effective implementation requires frequent application, due to new plant growth and wet weather, and mild weather, which restricts its usefulness in winter, when the most severe damage occurs. These are obviously high-maintenance options, but both were tested informally before they were discontinued.

4. *Fertility control:* A broad range of techniques and agents to reduce recruitment, including sterilization and hormone implants, have been attempted on an experimental basis. Reproductive inhibitors delivered by way of oral ingestion, surgical implants, and intramuscular injection have been researched primarily on domestic animals and, in a few cases, on feral horses and captive deer (Kirkpatrick and Turner 1988). Remote injections via dart may prove applicable to small insular herds that can be treated and then closely monitored. Due to sustained interest from animal welfare advocates, PPNP partially funded research by Kirkpatrick and Turner (1988) to test various darting protocols at the park. This demonstrated that techniques showing some success are both costly and labour-intensive, require a significant amount of training and skill, and demand that a very high percentage of deer need to be treated. Use of fertility control methods on free-ranging deer herds is impractical at PPNP.
5. *Supplemental feeding/planting programs:* Feeding programs supply non-native foods in an attempt to divert deer from utilizing natural vegetation. As a method for reducing impacts on natural vegetation, it is counterproductive, as it permits reproductive success beyond the limiting capacity of the habitat. Plantings or site rehabilitation is currently being used at PPNP to restore native vegetation communities in human-disturbed habitats. Continued high deer densities would preclude the success of long-term natural succession and require protection for the planted areas. Rehabilitated areas provide added food sources and habitat and thus increase the potential for deer reproductive success.
6. *Reintroduce predators:* This method would attempt to return the natural large predators to the park ecosystem. The already-present coyote *Canis latrans*, while a natural predator of deer and adaptable to urban settings, is not a consistently effective population control agent. The large natural areas in southern Ontario that once supported timber wolves *Canis lupus*, black bears *Ursus americanus*, and cougar *Puma concolor* no longer exist. Significant insurmountable public concerns would result from any suggestion of a large predator reintroduction program in the PPNP environs.
7. *Regulated hunting and culls:* Increased hunting pressure outside park boundaries is a herd control mechanism that has already been implemented by the province. A small percentage of the park deer population uses adjacent agricultural areas for foraging, and the local farming community encourages bow hunters (firearms are not allowed due to provincial restrictions) to hunt these animals. Culls are a substitute for predation that occurs in more naturally functioning ecosystems and have been proven to be an effective and efficient deer management tool. Although initial implementation costs can be moderately high, costs of subsequent smaller culls to maintain the reduced herd size are lower. Potential effects on park visitors and nearby residents can be effectively addressed.

On this basis, an initial herd reduction and subsequent maintenance culls were recommended and approved at the ministerial level for implementation at PPNP. This proven method would immediately alleviate browsing pressure on the park's vegetation, maintain consistency with other southern Ontario PHA management actions, and have lower ongoing implementation costs compared with other management strategies.

3.5 Implementation logistics

Ultimately, the cull option was confirmed at all four southern Ontario PHAs, and each site had to develop implementation strategies. The logistics differed somewhat at each site, but all had similar issues. For example:

1. *Human safety:* All four PHAs were wholly or partially closed during culling operations. PPNP was closed Monday to Friday and open Saturday and Sunday during herd culls. The local provincial police dog master was placed on standby to assist in removing from the park protesters who might threaten to infiltrate and disrupt the operation.
2. *Shooter safety:* All shooters were required to pass hunter safety and firearm competency tests. In PPNP, Park Warden staff undertake annual firearm proficiency training, and, because of national park legislation, they undertook the cull. The legislation at the other three PHAs allowed the use of members of the public and/or First Nations.
3. *Shooter preferences:* Similar procedures prevailed at all sites, but the targeting of young female deer that would contribute most to the future population growth was more difficult when hunters were used. This may have been due to the timing of the cull during the fall rut, at which time male deer are more susceptible, or it may have been due to the general reluctance of hunters to take does or young deer.
4. *Staff/resident safety:* At all four PHAs, detailed safety plans were developed to ensure that staff and park residents had a coordinated strategy to enable them to travel to and from the workplace and between work sites within the park.
5. *Veterinary services:* All four sites arranged veterinary services for the collection of morphological data from each deer carcass, such as age, body measurements, live and field dressed weights, presence of external/internal parasites and meningeal brain worm *Parelaphostrongylus tenuis*, as well as blood samples for Lyme disease.
6. *Utilization of meat, hides, and other products:* At PPNP, arrangements to use the culled deer had to be made. PPNP, and other sites if required, also had each carcass inspected at the abattoir and approved as fit for human consumption before distribution. Meat products were offered to First Nations, food banks, and other charitable organizations free of charge, although processing fees were paid by the recipient organization. Hides were distributed to Ontario First

Nations organizations through the provincial Ministry of Natural Resources network. Antlers, fetuses, and other parts attractive to the herbal medicine industry were returned to the park for dispersal.

3.6 Communication strategies

Until the late 1980s, Parks Canada's ungulate management program had been largely focused on the management of surplus bison *Bison bison* in Elk Island National Park, an entirely fenced and intensively managed national park near the city of Edmonton, Alberta, as well as the maintenance of disease-free wood bison *Bison bison athabascae* in Wood Buffalo National Park, straddling the border of Alberta and the Northwest Territories.

A process of briefing notes outlining the issue and possible options to Parks Canada management was necessary. In the fall of 1989, the park sponsored a workshop of various specialists to confirm the descriptions of the vegetation communities within the park and to establish management objectives for each of these communities (Landplan Collaborative Ltd. 1990b). The approved objectives linked the need to reverse the negative impacts of deer herbivory on certain vegetation communities to the park's purpose and objectives, which were outlined in the Point Pelee National Park Management Plan (Parks Canada 1995). Media lines were developed for the intense print, radio, and television reaction that was encountered. Specific community concerns, such as the legal constraints that dictated staff versus public hunting, were addressed through the media and personal contacts. The provision of deer ecology education and the need to address animal rights/ welfare concerns among various community interest groups were accomplished through a series of public meetings and school visits.

PPNP and the other three PHAs have "operationalized" their deer herd reduction programs as part of their site ecosystem management programs. All interest groups and stakeholders are advised of the cull operation immediately prior to commencement. As a result of the initial and ongoing implementation of communication strategies, negative reaction to recent culls has been negligible.

4. Results

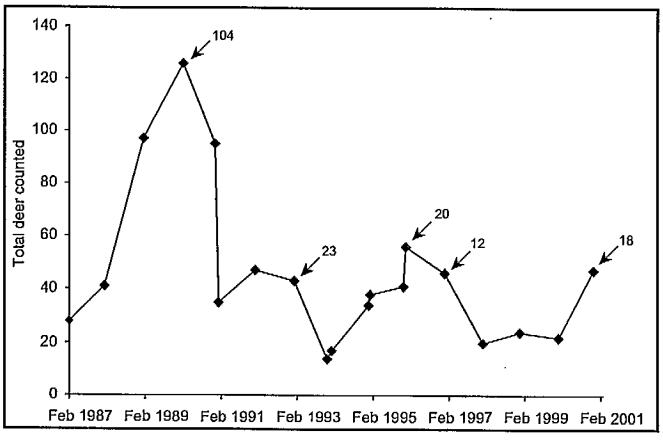
White-tailed deer became extirpated from PPNP in the early part of the 20th century and were subsequently reintroduced in 1941. By the early 1950s, several small culls were undertaken as a result of complaints of crop damage by apple orchard growers. Twenty-eight deer in total were culled in 1952, 1954, and 1956, leaving about 10 animals each year. From the mid-1950s to the mid-1970s, anecdotal accounts indicate that the herd numbered no more than 30 animals at any one time. By the late 1980s, the herd had expanded to over 120 animals. By the time the first cull was implemented in January 1991, there was a need to remove well over 100 animals from the population. The first staff cull removed 104 animals; the 1993 cull removed 23 animals; the 1996 cull 20 animals; the 1997 cull 12 animals; and the 2001 cull 18 animals. The decision point for each cull was reached when the annual aerial census indicated a herd size of more than 35 animals. Although PPNP has been successful in maintaining a somewhat stable deer population since 1991, deer numbers remain slightly higher than the desired density of 24–32 animals (Fig. 3). Vulnerable rare plant populations, Carolinian Forest succession plots, and soil (trail) disturbance continue to be monitored at PPNP.

At LPNWA, the deer populations peaked at approximately 550 animals at the time of the first public hunter cull in 1989. The herd has been stabilized at approximately 100 animals since the last cull in 1994, and that number serves as the decision point for any subsequent culls. Deer herd numbers are monitored on an ongoing basis; as well, breeding bird populations and 15 plant communities are monitored for effects from deer herbivory (J. Robinson, pers. commun.).

At RPP, deer populations were controlled through staff culls from 1912 until the early 1970s. In 1974, deer herd reductions were discontinued due to public opposition, and in the following 20 years the herd size grew to over 600 deer (Ontario Ministry of Natural Resources 2001). The first post-1970s cull, conducted in 1993 using First Nations shooters, removed 322 animals from the population. The next cull was conducted in 1998, when 96 animals were removed. Culls have occurred yearly since then, with 55, 42, 32, and 58 deer culled each year between 1999 and 2002, respectively. The density of deer in RPP should remain near 75 animals in order to protect unique vegetation communities in the park (R. Hart, pers. commun.). Monitoring of breeding bird populations, understory vegetation, and deer exclosures (established in 1978) to evaluate the response to reduced deer herbivory is ongoing.

At PPP, the herd size had grown to over 1000 animals by the mid-1990s. The first cull, conducted by First Nations shooters in 1998, removed 264 animals from the population. Four subsequent yearly culls have been conducted, removing 96, 94, 46, and 63 deer between 1999 and 2002, respectively. The present park population is around 300 deer, well above the desired density of 175 (T. Purdy, pers. commun.). Monitoring of the globally significant oak savannah vegetation community and the response to reduced deer pressure continues.

Figure 3
Aerial deer census results for Point Pelee National Park (1987–2000), showing the timing of culls (arrows) and number of animals killed



5. Conclusions

Initial herd reduction and subsequent maintenance culls are a largely successful resource management strategy to regulate white-tailed deer populations in PPNP and three other PHAs in southern Ontario. Ecological benefits for the unique floral and faunal communities within these four remnant natural areas were immediately apparent. Long-term monitoring will be required, as recovery of ecosystem components may take decades. Social benefits for local First Nations communities, public hunters, and, in the case of PPNP, the recipients of meat and hide products have been positive. The education and communication strategies associated with the culls have helped local residents better understand how these parks' ecosystems function. The process of justifying and implementing a deer herd management program in Haida Gwaii (Queen Charlotte Islands, British Columbia) should be similar to those that are being successfully undertaken in PPNP, RPP, PPP, and LPNWA over the last 15 years.

Literature cited

Canadian Parks Service. 1990. Issue analysis: Management options for reducing the effects of deer browsing in the context of approved vegetation management objectives. Canadian Parks Service, Natural Resource Conservation, Ontario Region, and Point Pelee National Park.

COSEWIC. 2002. Canadian species at risk, May 2002. Committee on the Status of Endangered Wildlife in Canada. 34 pp.

Dasmann, W. 1971. If deer are to survive. Stackpole Books, Harrisburg, Pennsylvania. 128 pp.

Dasmann, W. 1981. Wildlife biology. 2nd ed. John Wiley and Sons, New York. 203 pp.

Ellingwood, M.R.; Caturano, S.L. 1988. An evaluation of deer management options. Publication No. DR-11, New England chapter of The Wildlife Society and the Northeast Deer Technical Committee, Connecticut Department of Environmental Protection, Wildlife Bureau.

Ellingwood, M.R.; Spignesi, J.V. 1986. Management of an urban deer herd and the concept of cultural carrying capacity. Trans. Northeast Deer Tech. Comm. 22: 42–45.

Hutchinson, B.C.; Mosquin, T.; Ranta, W.B. 1988. White-tailed deer management plan for Point Pelee National Park. Environment Canada–Parks, Ontario Region, Cornwall, Ontario.

Kirkpatrick, J.F.; Turner, J.W., Jr. 1988. Contraception as an alternative to traditional deer management techniques. *In* S. Lieberman (ed.), Deer management in an urbanizing region. The Humane Society of the United States, Washington, D.C.

Landplan Collaborative Ltd. 1990a. The effects of deer browsing on the rare plants of Point Pelee National Park. Unpublished report, Canadian Parks Service, Cornwall, Ontario. 20 pp. + appendices.

Landplan Collaborative Ltd. 1990b. Vegetation management objectives. Point Pelee National Park. Canadian Parks Service, Ontario Region, Cornwall, Ontario. 46 pp.

Leggo, J. 1989. Development of bait stations for use in the chemical immobilization of white-tailed deer. Unpublished report, Point Pelee National Park, Leamington, Ontario. 23 pp.

Marquis, D.A.; Brennemann, R. 1981. The impact of deer on forest vegetation in Pennsylvania. General Technical Report NE-65, Northeastern Forest Experiment Station, Forest Service, U.S. Department of Agriculture, Radnor, Pennsylvania. 7 pp.

Matschke, G.H.; de Calesta, D.S.; Harder, J.D. 1984. Crop damage and control. Pages 647–654 *in* L.K. Halls (ed.), White-tailed deer ecology and management. A Wildlife Management Institute book. Stackpole Books, Harrisburg, Pennsylvania.

McCullough, D.R. 1979. The George Reserve deer herd: population ecology of a K-selected species. University of Michigan Press, Ann Arbor, Michigan. 271 pp.

McCullough, D.R. 1984. Lessons from the George Reserve, Michigan. Pages 211–242 *in* L.K. Halls (ed.), White-tailed deer ecology and management. A Wildlife Management Institute book. Stackpole Books, Harrisburg, Pennsylvania.

McCullough, G.B.; Robinson, J. 1988. Overbrowsing of vegetation by white-tailed deer on the Long Point National Wildlife Area. Unpublished report, Canadian Wildlife Service, Ontario Region, Ottawa, Ontario.

Mosquin, T. 1988. Monitoring of the Carolinian Forest of Point Pelee National Park. Part 1: Status descriptions and monitoring rationale. Environment Canada–Parks, Ontario Region, Cornwall, Ontario.

Ontario Ministry of Natural Resources. 2001. Rondeau Provincial Park vegetation management plan. Ontario Parks, Aylmer District Office, Aylmer, Ontario.

Parks Canada. 1995. Point Pelee National Park management plan. Parks Canada, Ontario Region, Department of Canadian Heritage, Cornwall, Ontario.

High herbivore density and boreal forest ecology: white-tailed deer on Anticosti Island

Steeve D. Côté, Christian Dussault, Jean Huot, François Potvin, Jean-Pierre Tremblay, and Vanessa Viera

Abstract

Anticosti Island, in the Gulf of St. Lawrence, Quebec, can be considered a natural laboratory to address the direct and indirect effects of overabundant herbivores on plants and ecosystem integrity. White-tailed deer *Odocoileus virginianus* were introduced to Anticosti Island at the end of the 19th century, and, in the absence of predators, their numbers increased rapidly. Deer density is currently estimated at >15 deer/km^2. Significant damage to the vegetation was reported as early as the 1930s. By now, all plant species preferred by deer have been eliminated from the understory, and species composition and vegetation structure in the herbaceous layer have been altered. Deer browsing prevents the natural regeneration of balsam fir *Abies balsamea* stands, which are progressively replaced by forests dominated by white spruce *Picea glauca*. The balsam fir is a key species for white-tailed deer on Anticosti, where it represents over 70% of the deer winter diet. Most fir seedlings are browsed in summer, preventing them from recruiting into saplings. In the near future, these changes are likely to affect the integrity of the island ecosystems, as well as the deer population itself, which represents a valuable resource, because deer hunting is an essential part of the island's economy. An Industrial Research Chair, equally funded by the Natural Sciences and Engineering Research Council of Canada (NSERC) and by Produits forestiers Anticosti Inc., has been created at Laval University to investigate deer–forest relationships. The main objective of the Chair is to develop forest and wildlife management methods suited to high deer densities. The research program focuses on 1) the impact of high animal densities on forest ecosystems; 2) habitat selection and foraging behaviour of deer; 3) developing silvicultural and browsing control practices adapted to high herbivore densities; and 4) developing integrated tools to manage forest biological resources. This paper summarizes the current situation on Anticosti Island and describes the main research projects of the NSERC–Produits forestiers Anticosti Industrial Research Chair in integrated management of forest resources.

1. Introduction

Forest resources, mainly wood products and wildlife, have an enormous potential for economic development in Canada. For sustainable development, the use of these resources has to be compatible with maintaining the biodiversity and the natural processes characteristic of forest ecosystems. Managing for these objectives is complicated where native or introduced ungulates jeopardize natural habitat regeneration (Gill 1992; Hobbs 1996; Kielland and Bryant 1998).

This issue is increasingly prominent in many parts of the world, in particular within the distribution range of white-tailed deer *Odocoileus virginianus* (Tilghman 1989; Conover 1997; Waller and Alverson 1997; Rooney 2001), black-tailed/mule deer *O. hemionus* (Sharpe 2002), Muntjac deer *Muntiacus reevesi* (Cooke and Farrell 2001), and Sika deer *Cervus nippon* (Akashi and Nakashizuka 1999) and in areas where moose *Alces alces* have no natural predators, such as in Newfoundland (McLaren and Peterson 1994; McLaren 1996; McLaren et al. 2000) or in Scandinavia (Edenius et al. 1995; Cederlund and Bergström 1996). In Sweden, for example, the damage caused every year by cervids to the coniferous forest is estimated at US$340 million (Bergström et al. 1992). The economic losses caused by white-tailed deer overabundance in the United States are estimated to be in excess of US$1 billion annually (P.D. Keyser, pers. commun.).

High herbivore densities can also have numerous direct or indirect effects on other organisms in ecosystems (Huntly 1991; Fuller and Gill 2001; Rooney and Waller 2003), such as small mammals (Flowerdew and Ellwood 2001), birds (Fuller 2001; Perrins and Overall 2001), and invertebrates (Feber et al. 2001; Stewart 2001). They may also affect competitive interactions between plants and favour some species over others (Huntly 1991). Such situations have prompted concern in several national parks in Canada (Sinclair 1998) and in the United States (Boyce 1998; Porter and Underwood 1999) where plant diversity and productivity have decreased as a result of herbivory. Given that hunting pressure in Canada is decreasing almost everywhere, similar situations are likely to become increasingly frequent, especially if current trends of climate warming persist.

Anticosti Island provides an ideal situation to study questions related to high densities of herbivores. White-tailed deer were introduced at the end of the 19th century, and today deer densities are estimated to be >15 deer/km^2. Vegetation structure and diversity on Anticosti have been

deeply modified since deer were introduced. In the fall of 2001, an Industrial Research Chair, equally funded by the Natural Sciences and Engineering Research Council of Canada (NSERC) and Produits forestiers Anticosti Inc., was officially created at Laval University (Quebec City) to study deer–forest relationships on Anticosti Island. This paper explains how deer ecology is intimately related to forest regeneration on Anticosti and describes the main research projects of the Chair.

2. Anticosti background

Located in the Gulf of St. Lawrence, Quebec, Anticosti Island is 7943 km² in area (length 220 km, maximum width 56 km). The topography is relatively flat, with a mean elevation of only 126 m. The bedrock is formed of Silurian and Ordovician limestone. Postglacial marine sediments cover the lowlands as well as the shoreline, whereas the interior is covered by glacial moraine. The subboreal maritime climate is characterized by cool summers and relatively mild winters. The mean temperature in January is about –10°C, and in July, 15°C. In general, snow is abundant, and total accumulation is about 20% greater than in other areas where white-tailed deer are found in Quebec (Huot 1982).

The forests of the island belong to the balsam fir–white birch bioclimatic domain of the lower and eastern boreal region (Grondin et al. 1996). The most common stands are the white spruce *Picea glauca*, balsam fir *Abies balsamea*, and black spruce *Picea mariana* stands. White birch *Betula papyrifera*, quaking aspen *Populus tremuloides*, balsam poplar *P. balsamifera*, and larch *Larix laricina* occur only sporadically. In the eastern part of the island, forests alternate with extensive peatlands. In the past, the major natural perturbations have been fire, insect outbreaks, and windfalls. The conditions found on the island have favoured a rich and diverse herbaceous layer, with several species that have a very restricted distribution range.

The island fauna included originally only seven species of mammals: the black bear *Ursus americanus*, the river otter *Lutra canadensis*, the red fox *Vulpes vulpes*, the American marten *Martes americana*, the deer mouse *Peromyscus maniculatus*, and two species of bats (*Myotis lucifugus* and *M. septentrionalis*). The main introduced species are white-tailed deer, moose, snowshoe hare *Lepus americanus*, beaver *Castor canadensis*, and muskrat *Ondatra zibethicus* (Newsom 1937; Cameron 1958). The black bear, the only potential predator of white-tailed deer, is probably extinct on the island.

Anticosti Island remained a wild and mostly uninhabited island until 1895, when it was purchased by a wealthy French businessman who tried to introduce several game species: white-tailed deer was the only one that became widespread. Among introductions that failed were bison *Bison bison* and elk *Cervus elaphus*. Moose, introduced at the same time, has remained at low densities. During the 20th century, several forest companies owned Anticosti Island. Eventually, in 1974, the island was purchased by the Quebec government. The island has been divided into five territories on which different managers (public, private, or communities) run sport hunting. Except for the recently created Anticosti Park (572 km²), most of the island is opened to deer hunting (91% of the area). The only village, Port-Menier, is located at the western end of the island. Although its population can double in summer because of seasonal work, the permanent population is about 250 people. The main economic activities of the island are sport hunting of white-tailed deer and forestry.

3. Deer on Anticosti Island and their impact

About 200 white-tailed deer were introduced on Anticosti Island in 1896 and 1897. In the absence of predators, they multiplied rapidly, despite the boreal nature of the forest. The first reliable population estimates were obtained at the end of the 1980s, when aerial surveys estimated the total deer population at 120 000 animals (15/km²) (Potvin et al. 1991). Since then, deer have remained abundant in spite of fluctuations related to winter severity. Today, however, deer winter habitat shows obvious signs of degradation. The animals normally use all of their fat reserves during winter and can also use up to 40% of their proteins during harsh winters (Huot 1982; Côté, unpubl. data). The growth rate of fawns and the proportion of twins on Anticosti Island are among the lowest recorded in North America (Goudreault 1978; Huot 1982; Lesage et al. 2001).

The first major deer-induced changes in the vegetation were identified in the 1920s to 1930s. Some broad-leaved shrubs, formerly abundant, were already practically eliminated (Pimlott 1963; Marie-Victorin and Rolland-Germain 1969). During the following decades, several researchers reported major modifications in the woody and herbaceous vegetation layers and suggested increasing hunting pressure to reduce damage by deer (Leopold et al. 1947; Pimlott 1954). However, despite the major infrastructures in place today, sport hunters kill only 8% of the estimated population annually, not enough to achieve any population control (Gingras 2002).

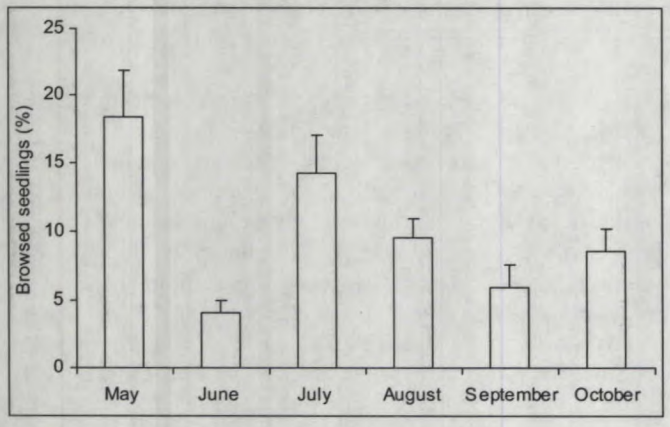
Nowadays, most herbaceous plants and shrubs browsed by deer either have vanished or are dramatically reduced in abundance. In the balsam fir stands, these species are replaced by species that are less palatable to deer or that better sustain heavy browsing, such as thistles and grasses. The construction of exclosures has, on the other hand, demonstrated that several of the species severely affected by deer are still present on the island, often in the form of seed banks in the soil, allowing them to reappear as soon as browsing pressure is relaxed (Potvin et al. 2000; Figs. 1 and 2).

Forest composition and structure have been widely modified by deer. The regeneration of the fir stands, a key habitat for deer winter survival on Anticosti Island (Boulet 1980; Huot 1982; Lefort 2002), is currently compromised. Balsam fir seedlings are browsed year-round when not protected by snow (Fig. 3). On top of natural seedling mortality, browsing increases yearly fir seedling mortality by about 48% in young clearcuts and by about 26% in forest stands (Potvin and Laprise 2002). This lack of recruitment modifies the forest succession, and balsam fir is progressively replaced by white spruce, a tree species eaten little or not at all by deer (Huot 1982). The study of successional series and

Figure 1
An exclosure of 0.09 ha installed in 1983 in a clearcut on Anticosti Island to show the effect of white-tailed deer browsing on the vegetation. The regeneration inside the exclosure is dense and dominated by white birch and balsam fir.

Figure 2
Quick response of the vegetation on Anticosti Island to the absence of browsing by white-tailed deer, as shown by this exclosure built 5 years ago in a clearcut.

Figure 3
Monthly browsing rates on balsam fir seedlings in summer in recent clearcuts on Anticosti Island (Potvin and Laprise 2002). During each survey, all browsed seedlings were removed. Our data therefore indicate the percentage of seedlings that were browsed during the month immediately preceding the survey.



of historical documents suggests that the surface covered by balsam fir forests has been reduced by about 50% during the last 100 years on Anticosti Island (Potvin et al. 2003). Surprisingly, the aging of the fir forest could have a short- or medium-term positive effect on deer population, because old firs are more easily blown down by strong winds, and these fallen trees provide a temporary, albeit nonrenewable, food supply to deer. Currently, balsam fir makes up about 70% of the deer diet in winter (Lefort 2002). The shrub layer is entirely missing in the balsam fir forests, where it should be as abundant and diversified as on the Mingan Islands, where abiotic conditions are similar to those on Anticosti Island but from which deer are absent (Fig. 4). *Rubus*, *Taxus*, *Goodyera*, and *Sorbus* are examples of genera found on the Mingan Islands but not found on Anticosti Island outside of exclosures.

Since 1995, several logging practices have been tried to help balsam fir forest to regenerate. Unfortunately, data so far indicate that all of the cut blocks are dominated by regenerating white spruce instead of fir. Since 2000, all new cut blocks on the island are fenced (Fig. 5), and deer density in these areas is reduced by sport hunting. This costly and temporary solution aims at preventing browsing and favouring fir regeneration. Therefore, it is essential to develop alternative methods to allow the reestablishment of balsam fir or mixed balsam fir–white spruce stands. At a medium- or long-term temporal scale, the current high deer population is likely to generate negative effects on the other plant or animal species associated with the fir forests or even on the overall ecological processes of these forests. In addition, deer hunting, the main economic activity on the island, may also be negatively affected if fir stands do not regenerate.

Figure 4
Occurrence (in 80 10-m^2 plots) of ligneous plants at the shrub stage (30–200 cm in height) in the fir forests studied on the Mingan Islands where white-tailed deer is absent. On Anticosti Island, none of these species has been recorded at the shrub stage (in 80 10-m^2 plots). *Sorbus americana* is American mountain ash; *Taxus canadensis* is Canada yew; *Acer spicatum* is mountain maple; and *Rubus idaeus* is common red raspberry.

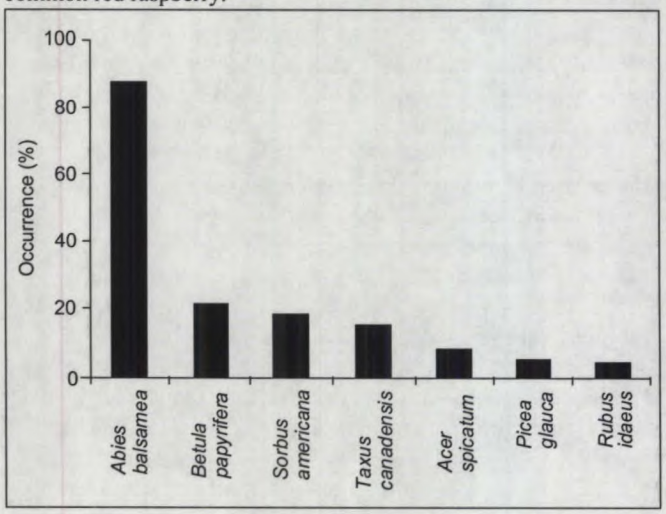


Figure 5
Installation of game fences 3.5 m in height around all clearcuts since 2000. The number of deer inside the enclosure is reduced by sport hunting to allow fir regeneration.

4. Objectives and research program of the NSERC-Produits forestiers Anticosti Industrial Research Chair

The overall objective of the Chair is to develop forest and wildlife management methods adapted to high deer densities. The features of Anticosti Island make it a natural laboratory, allowing the development of a research program at the scale of the ecosystem. Classified as a wildlife management area, the island offers opportunities to experiment with new silvicultural methods. The nearby Mingan archipelago offers a good control site from which deer are absent.

The research program includes four main themes that cover fundamental and applied research aspects related to sustainable development of forest resources at high deer density:

1. impact of high animal densities on forest ecosystems;
2. habitat selection and foraging behaviour of deer;
3. defining and developing silvicultural and browsing control strategies that are applicable in a context of high herbivore densities; and
4. defining and developing integrated tools to manage biological forest resources.

Themes 1 and 2 aim at understanding the dynamics of deer–forest interactions and identifying the mechanisms allowing deer to limit forest regeneration. We will use the knowledge acquired by our research to design themes 3 and 4.

4.1 Theme 1: Impact of high animal densities on forest ecosystems

4.1.1 Project 1: Boreal balsam fir forest regeneration in relation to white-tailed deer browsing pressure

The regeneration dynamics of a forest stand rests on equilibrium processes that allow no successional changes in space and time (Veblen 1992). Communities tend to retain their composition or to recover it after a perturbation (Kimmins 1987). In balsam fir and white spruce stands, this balance is maintained by a bank of seedlings (Frank 1990; Nienstaedt and Zasada 1990). In mature forests, seedlings are suppressed until a local perturbation allows light to reach the understory (Harper 1977; Morin and Laprise 1997).

The main objective of this project is to predict the regeneration dynamics of the humid boreal balsam fir forest in relation to white-tailed deer browsing intensity by 1) studying the effect of deer density on the installation, growth, and survival of balsam fir; 2) verifying the effect of deer density on deer body condition; 3) assessing how and when a balance can be reached between browsing and regeneration and the related thresholds in deer densities; and 4) developing a model for the dynamics of the boreal balsam fir forest regeneration that incorporates the effects of white-tailed deer.

To address these objectives, we established an experiment controlling for browsing pressure, as advocated by Hester et al. (2001) and Schmitz and Sinclair (1997), to identify density thresholds compatible with tree and shrub regeneration and to understand the relationship between browsing pressure and the recruitment of seedlings and saplings. Such experiments have already been tested in deciduous forests (Tilghman 1989), but not, as far as we know, in boreal forests. Our experiment consists of three blocks, each subdivided into four fenced units varying in size from 10 to 40 ha and including different deer densities. In each enclosure, we logged about 50% of the area, left the rest as untouched pockets of natural forests, and applied one of four browsing treatments (0, 7.5, 15, or ~20–25 deer/km^2). The response of the vegetation to treatments (recruitment, growth and survival of seedlings, cover and biomass of herbaceous vegetation) is estimated by regular vegetation sampling in 480 permanent plots, randomly distributed in the enclosures. Close to 4000 fir seedlings have been individually marked.

4.2 Theme 2: Habitat selection and foraging behaviour of deer

4.2.1 Project 2: Foraging behaviour and activity budgets of deer at different densities

To understand the mechanisms that generate deer impact on forest regeneration, it is essential to study their behaviour (Miller 1997; Miller and Ozoga 1997). In particular, it is necessary to assess whether deer adopt specific behaviours to survive in a context of high population density. Deer could, for instance, compensate for low forage abundance at high densities by spending more time feeding

or by being less selective (Borkowski 2000). Feeding on plants of poorer quality may also imply an increase in rumination time (Westoby 1974; Murden and Risenhoover 1993).

To identify the influence of population density on foraging strategies and activity budgets of white-tailed deer on Anticosti, we use activity-recording radio collars installed on deer introduced in the experimental enclosures. Deer are located by triangulation during both day and night. We compare vegetation cover and biomass between the locations used by deer and habitat availability in the enclosure. We use automated telemetry receivers that continuously record activity, allowing us to assess the effect of population density on the duration and frequency of active periods (feeding and moving) and inactive periods (resting and ruminating).

4.2.2 Project 3: Habitat selection of white-tailed deer at different spatial scales

The main objective of this project is to assess how habitat selection by white-tailed deer is affected by vegetation composition at a fine scale, as well as by the structure of the forest mosaic at a large scale. As suggested by Johnson (1980) and Potvin et al. (1999), we study habitat selection at the scales of the forest landscape, of the home range, and of the microhabitat. We also examine daily and seasonal variation in habitat use. To better understand the effects of deer on vegetation regeneration and deer habitat needs, we study movements of individual deer under natural conditions. These observations give us a better understanding of the relationships between herbivores and their food resources (Hester et al. 2001).

We use global positioning system collars fitted on adult females between June and November (2001: $n = 8$; 2002: $n = 12$) and January and May (2002: $n = 8$). Vegetation surveys and forage biomass estimates are conducted in the areas most and least used by deer within home ranges and compared with adjacent areas located outside home ranges in order to better define the characteristics of the plant communities selected by deer. Our preliminary results indicate that deer use all available habitats, including peatlands in summer, but seem to prefer forest clearcuts and forest peatland edges (A. Massé and Côté, unpubl. data).

4.2.3 Project 4: Influence of winter diet quality on body condition, feeding behaviour, and social interactions of white-tailed deer

On Anticosti Island, the winter diet of deer consists of 70% balsam fir, 20% white spruce, and 10% arboreal lichens (Lefort 2002). A significant proportion of the winter fir browse is made available by windthrows (Potvin et al. 2000). This source of food, however, will likely disappear in the medium term, as deer are preventing fir regeneration, in which case deer will likely have to rely more on white spruce, the only other available browse species on the island. This species is generally avoided by white-tailed deer (Lefort 2002), although the reason why spruce is only lightly used remains unclear.

This part of the research assesses the nutritive value of balsam fir and white spruce and measures the effect of winter diet quality on deer body condition and social behaviour. We estimate the nutritive value and chemical defences of both species of trees from branches collected on several sites (Robbins et al. 1987). We also experimentally manipulate the diet of about 24 captive deer between December and April. The social rank of each deer is identified at the beginning of the experiment, when the deer are all kept together. Afterwards, deer are separated among three 1.2-ha enclosures. We manipulate their winter diet by changing the proportion of fir (preferred food on Anticosti) and white spruce in the three enclosures. The effects of diet quality on deer body condition are studied with the help of indices, such as body mass and snow urine enzyme ratios, that indicate when deer are starting to utilize their protein reserves (Garrott et al. 1996; Vagnoni et al. 1996; DelGiudice et al. 2000). We analyze aggressive interactions between the animals to estimate the influence of winter diet quality on social dominance and social interaction rates (Côté 2000). No study has experimentally estimated how social rank varies in relation to changes in body condition during winter. One could predict that energy allocated to aggressive behaviours should decrease with decreasing body condition and that social rank would be negatively affected. Our preliminary results suggest that dominant fawns are more aggressive than subordinates and that aggressiveness is positively related to body mass throughout the winter (J. Taillon and Côté, unpubl. data). At the end of the experiment, all deer are brought back together in the same enclosure to verify whether the social ranking among individuals has remained stable or if diet quality has affected social rank through its effect on body condition. Our data so far suggest that dominant deer survive better than subordinates and that the social rank of deer that survive the winter is independent of diet and similar to their rank in early winter (J. Taillon and Côté, unpubl. data).

An applied objective of this work is to estimate the minimum quality of winter diet that is compatible with maintaining acceptable deer body condition. The results of this study will allow us to better understand and predict the effects of the progressive replacement of balsam fir forests by white spruce forests on the body condition and, eventually, population dynamics of white-tailed deer on Anticosti Island.

4.3 Theme 3: Defining and developing silvicultural and browsing control strategies that are applicable in a context of high herbivore densities

4.3.1 Project 5: Experimental large-scale clearcuts with protection of regeneration and soils

On Anticosti Island, deer prevent the natural regeneration of browsed species after clearcutting (Potvin and Laprise 2002). Reducing habitat suitability to deer could, however, reduce browsing. In areas where predators are present, white-tailed deer normally avoid areas that lack easily accessible cover (Drolet 1978; Williamson and Hirth 1985). If deer avoid the central part of large cut blocks, balsam fir and other species of deer-preferred forage may regenerate there. Hence, this project is designed to verify whether browsing pressure decreases in relation to increasing

distance to the edge in large cut blocks. To achieve this, we installed clusters of permanent plots distributed at different distances from the edge of seven 300-ha clearcuts. Control plots are situated inside exclosures to protect them from browsing. Surveys of vegetation, woody debris, and soils are performed to measure regeneration and the effect of environmental factors. Our results indicate that browsing pressure is high and similar in the centre and near the edge of large clearcuts (Potvin and Laprise 2002).

4.3.2 Project 6: Experimental logging using the seed tree method and strip cutting with soil scarification

A few balsam firs could escape browsing if seedlings were so abundant that deer could not browse them all. Clearcuts with seed tree retention or strip cutting, successfully used in black spruce forests (Prévost 1997), might facilitate such a mechanism. To test this hypothesis, we have created an experiment with seed tree reserves and strip cutting, testing different patch sizes of remnant forests and various strip widths. Permanent plots and exclosures have been laid out in different locations to measure the impact of deer browsing in cut blocks, some parts of which were scarified. This treatment should create seedbeds favourable to the germination of certain species, such as the white birch (Prévost 1997). The colonization of these sites by plants that are preferred by deer may reduce browsing pressure on fir and allow a certain proportion of fir seedlings to survive and grow above the reach of deer.

4.4 Theme 4: Defining and developing integrated tools to manage biological forest resources

4.4.1 Project 7: Assessing sport hunting as a management tool to reduce the abundance of local deer populations

At the scale of the island, it is not possible to reduce and stabilize deer population at a lower level through hunting alone (Lesage et al. 2000). However, intense and persistent hunting could reduce deer numbers in a limited area. Both we and others have found that females and their female offspring tend to use the same sites from year to year (Lesage et al. 2000; Kilpatrick et al. 2001). Significant hunting pressure targeted at this segment of the population could generate a local reduction of deer density, if immigration into the area is limited.

To estimate the potential of intensive hunting as a management tool to locally reduce the reproductive segment of the deer population and to favour natural tree regeneration, we identified four specific objectives: 1) estimate the efficiency of hunting to locally reduce female densities; 2) estimate the effect of density reduction on tree (seedlings), shrub, and herbaceous regeneration; 3) estimate the effect of density reduction on body condition, growth, and productivity of deer; and 4) assess the relationship between deer density and indices of hunter satisfaction and hunting success. It is important to identify the threshold in deer density below which hunter motivation is significantly reduced. This information would allow us to better assess the potential of female hunting as a management tool.

We defined a 20-km^2 hunting area in each of the five hunting units of the island and estimated deer density in each area by aerial surveys just before the hunting season. Our objective, achieved in all areas, was to reduce antlerless deer density by 50% during the first year of the project. Aerial surveys will be conducted again in the second year of the project and at the end of the experiment (2007). In the meantime, pellet counts will be used to estimate relative density variation among years. In order to measure the changes in the vegetation in the experimental hunting areas and in adjacent control areas, a network of permanent plots and small exclosures has been laid out during summer 2002. We compare body condition (Huot 1982), skeletal size, productivity (ovarian scars; Langvatn et al. 1994), and age (from teeth cement growth rings) of deer hunted in the experimental and in the control areas. Hunting statistics are used to estimate hunting success. Hunters are also interviewed to record their level of satisfaction in terms of their hunting experience.

5. A broader perspective

Although the negative effect of deer browsing on the vegetation is chronic on Anticosti Island, similar situations have developed in southern Quebec and in several other regions of northeastern North America. Whereas a few years ago wildlife managers were focusing on the protection of deer habitat from forestry practices, more and more concern is now expressed about the consequences of overabundant deer on plant diversity and forest regeneration. Research focus should be modified to address these new issues and management challenges.

Anticosti Island is an ideal site to study plant–herbivore interactions within an integrated resource management perspective. The whole territory is under specific forestry and hunting regulations that facilitate the implementation of experiments of integrated resource management. In addition, the industrial partner of the Chair is prepared to experiment with new forest harvesting methods, and wildlife and forest managers play an active role in defining and implementing the research program. In the near future, we are planning to implement several other research projects on the management of deer populations, the ecology of boreal forests, and the preservation of biodiversity. The context offered by the NSERC–Produits forestiers Anticosti Industrial Research Chair allows the realization of research projects that span periods of time long enough to measure real effects over realistic spatial scales.

Acknowledgements

We thank the Research Group on Introduced Species for its invitation to present this paper at its conference held in Queen Charlotte City, British Columbia. We would also like to thank for their constant efforts the graduate students of the NSERC–Produits forestiers Anticosti Industrial Research Chair: M.-L. Coulombe, S. Lefort, A. Massé, D. Sauvé, A. Simard, J. Taillon,

J.-P. Tremblay, and V. Viera, as well as the following researchers and people who contribute to the research activities of the Chair: P. Beaupré, L. Bélanger, L. Breton, C. Camiré, S. De Bellefeuille, D. Duteau, A. Gingras, G. Laprise, C. Malenfant, D. Morin, G. Picard, D. Pothier, M. Prévost, and B. Rochette. Several tens of field assistants take part in the work done on the island, and we thank them. Our research activities were made possible through the support of the following organizations: the Natural Sciences and Engineering Research Council of Canada, Produits forestiers Anticosti Inc., the Fonds québécois de la recherche sur la nature et les technologies, Laval University, the Centre d'études nordiques, the Ministry of Natural Resources of Quebec, and the Société de la faune et des parcs du Québec.

Literature cited

Akashi, N.; Nakashizuka, T. 1999. Effects of bark-stripping by Sika deer (*Cervus nippon*) on population dynamics of a mixed forest in Japan. For. Ecol. Manage. 113: 75–82.

Bergström, R.; Huldt, H.; Nilsson, U. 1992. Swedish game—Biology and management. Svenska Jägerförbundet/media, Uppsala, Sweden.

Borkowski, J. 2000. Influence of the density of a Sika deer population on activity, habitat use, and group size. Can. J. Zool. 78: 1369–1374.

Boulet, M. 1980. Bilan énergétique du cerf de Virginie à l'île d'Anticosti durant l'hiver. M.Sc. thesis, Department of Biology, Laval University, Quebec City, Quebec. 204 pp.

Boyce, M. 1998. Ecological-process management and ungulates: Yellowstone's conservation paradigm. Wildl. Soc. Bull. 26: 391–398.

Cameron, A.W. 1958. Mammals of the islands in the Gulf of the St. Lawrence. National Museum of Canada, Department of Northern Affairs and Natural Resources, Ottawa, Ontario. 165 pp.

Cederlund, G.; Bergström, R. 1996. Trends in the moose–forest system in Fennoscandia, with special reference to Sweden. Pages 265–281 *in* R.I. Miller (ed.), Conservation of faunal diversity in forested landscapes. Chapman & Hall, London, U.K.

Conover, M.R. 1997. Monetary and intangible valuation of deer in the United States. Wildl. Soc. Bull. 25: 298–305.

Cooke, A.S.; Farrell, L. 2001. Impact of Muntjac deer (*Muntiacus reevesi*) at Monks Wood National Nature Reserve, Cambridgeshire, eastern England. Forestry 74: 241–250.

Côté, S.D. 2000. Dominance hierarchies in female mountain goats: stability, aggressiveness and determinants of rank. Behaviour 137: 1541–1566.

DelGiudice, G.D.; Kerr, K.D.; Mech, L.D.; Seal, U.S. 2000. Prolonged winter undernutrition and the interpretation of urinary allantoin:creatinine ratios in white-tailed deer. Can. J. Zool. 78: 2147–2155.

Drolet, C.-A. 1978. Use of forest clear-cuts by white-tailed deer in southern New Brunswick and central Nova Scotia. Can. Field-Nat. 92: 275–282.

Edenius, L.; Danell, K.; Nyquist, H. 1995. Effects of simulated moose browsing on growth, mortality, and fecundity in Scots pine: Relations to plant productivity. Can. J. For. Res. 25: 529–535.

Feber, R.E.; Brereton, T.M.; Warren, M.S.; Oates, M. 2001. The impacts of deer on woodland butterflies: the good, the bad and the complex. Forestry 74: 271–276.

Flowerdew, J.R.; Ellwood, S.A. 2001. Impacts of woodland deer on small mammal ecology. Forestry 74: 277–287.

Frank, R.M. 1990. *Abies balsamea* (L.) Mill. Pages 26–35 *in* R.M. Burns and B.H. Honkala (eds.), Silvics of North America. Vol. 1. Conifers. Forest Service, U.S. Department of Agriculture, Washington, D.C.

Fuller, R.J. 2001. Responses of woodland birds to increasing numbers of deer: a review of evidence and mechanisms. Forestry 74: 289–298.

Fuller, R.J.; Gill, R.M.A. 2001. Ecological impacts of deer in woodland. Forestry 74: 189–192.

Garrott, R.A.; White, P.J.; Vagnoni, D.B.; Heisey, D.M. 1996. Purine derivatives in snow-urine as a dietary index for free-ranging elk. J. Wildl. Manage. 60: 735–743.

Gill, R.M.A. 1992. A review of damage by mammals in north temperate forests: 1. Deer. Forestry 65: 145–169.

Gingras, A. 2002. Plan de gestion du cerf de Virginie 2002–2008, Zone 20—Anticosti. Société de la faune et des parcs du Québec, Direction de l'aménagement de la faune de la Côte-Nord, Sept-Îles, Quebec. 21 pp.

Goudreault, F. 1978. Reproduction et dynamique de la population de cerf de Virginie de l'île d'Anticosti. Atelier sur le cerf de Virginie, île d'Anticosti, Direction de la recherche faunique, Ministère du tourisme, de la chasse et de la pêche, Anticosti, Quebec.

Grondin, P.; Ansseau, C.; Bélanger, L.; Bergeron, J.-F.; Bergeron, Y.; Bouchard, A.; Brisson, J.; De Grandpré, L.; Gagnon, G.; Lavoie, C.; Lessard, G.; Payette, S.; Richard, P.J.H.; Saucier, J.-P.; Sirois, L.; Vasseur, L. 1996. Écologie forestière. Pages 134–279 *in* Ordre des ingénieurs forestiers du Québec, Manuel de foresterie. Laval University Press, Ste. Foy, Quebec.

Harper, J.L. 1977. Population biology of plants. Academic Press, London, U.K. 892 pp.

Hester, A.J.; Edenius, L.; Buttenschon, R.M.; Kuiters, A.T. 2001. Interactions between forests and herbivores: the role of controlled grazing experiments. Forestry 73: 381–391.

Hobbs, N.T. 1996. Modification of ecosystems by ungulates. J. Wildl. Manage. 60: 695–713.

Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. Annu. Rev. Ecol. Syst. 22: 477–503.

Huot, J. 1982. Body condition and food resources of white-tailed deer on Anticosti Island, Québec. Ph.D. thesis, University of Alaska, Fairbanks, Alaska. 239 pp.

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61: 6571.

Kielland, K.; Bryant, J.P. 1998. Moose herbivory in taiga: Effects on biogeochemistry and vegetation dynamics in primary succession. Oikos 82: 377–383.

Kilpatrick, H.J.; Spohr, S.M.; Lima, K.K. 2001. Effects of population reduction on home ranges of female white-tailed deer at high densities. Can. J. Zool. 79: 949–954.

Kimmins, J.P. 1987. Forest ecology. Macmillan, New York. 531 pp.

Langvatn, R.; Bakke, Ø.; Engen, S. 1994. Retrospective studies of red deer reproduction using regressing luteal structures. J. Wildl. Manage. 58: 654–663.

Lefort, S. 2002. Habitat hivernal du cerf de Virginie (*Odocoileus virginianus*) à l'île d'Anticosti. M.Sc. thesis, Laval University, Ste. Foy, Quebec. 101 pp.

Leopold, A.; Sowls, L.K.; Spencer, D.L. 1947. A survey of overpopulated deer range in the United States. J. Wildl. Manage. 11: 162–177.

Lesage, L.; Crête, M.; Huot, J.; Dumont, A.; Ouellet, J.-P. 2000. Seasonal home range size and philopatry in two northern white-tailed deer populations. Can. J. Zool. 78: 1930–1940.

Lesage, L.; Crête, M.; Huot, J.; Ouellet, J.-P. 2001. Evidence for a trade-off between growth and body reserves in northern white-tailed deer. Oecologia 126: 30–41.

Marie-Victorin, f. é. c. and f. é. c. Rolland-Germain. 1969. Flore de l'Anticosti-Minganie. University of Montreal Press, Montreal, Quebec. 527 pp.

McLaren, B.E. 1996. Plant-specific response to herbivory: simulated browsing of suppressed balsam fir on Isle Royale. Ecology 77: 228–235.

McLaren, B.E.; Peterson, R.O. 1994. Wolves, moose, and tree rings on Isle Royale. Science 266: 1555–1558.

McLaren, B.E.; Mahoney, S.P.; Porter, T.S.; Oosenbrug, S.M. 2000. Spatial and temporal patterns of use by moose of pre-commercially thinned, naturally-regenerating stands of balsam fir in central Newfoundland. For. Ecol. Manage. 133: 179–196.

Miller, K.V. 1997. Considering social behaviour in the management of overabundant white-tailed deer population. Wildl. Soc. Bull. 25: 279–281.

Miller, K.V.; Ozoga, J.J. 1997. Density effects on deer socio-biology. Pages 136–150 *in* W.J. McShea, H.B. Underwood, and J.H. Rappole (eds.), The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C.

Morin, H.; Laprise, D. 1997. Seedling bank dynamics in boreal balsam fir forests. Can. J. For. Res. 27: 1442–1451.

Murden, S.B.; Risenhoover, K.L. 1993. Effects of habitat enrichment on patterns of diet selection. Ecol. Appl. 3: 497–505.

Newsom, W.M. 1937. Mammals on Anticosti Island. J. Mammal. 18: 435–442.

Nienstaedt, H.; Zasada, J.C. 1990. *Picea glauca* (Moench) Voss. Pages 204–226 *in* R.M. Burns and B.H. Honkala (eds.), Silvics of North America. Vol. 1. Conifers. Forest Service, U.S. Department of Agriculture, Washington, D.C.

Perrins, C.M.; Overall, R. 2001. Effect of increasing numbers of deer on bird populations in Wytham Woods, central England. Forestry 74: 299–309.

Pimlott, D.H. 1954. Deer-range conditions on Anticosti Island. Newfoundland Department of Mines and Resources, St. John's, Newfoundland. 22 pp.

Pimlott, D.H. 1963. Influence of deer and moose on boreal forest vegetation in two areas of Eastern Canada. Pages 105–116 *in* Transactions of the VIth Congress of the International Union of Game Biologists. The Nature Conservancy, Bournemouth, London, U.K.

Porter, W.F.; Underwood, H.B. 1999. Of elephants and blind men: Deer management in the U.S. National Parks. Ecol. Appl. 9: 3–9.

Potvin, F.; Laprise, G. 2002. Suivi de la banque de semis de sapin baumier sur l'île d'Anticosti en relation avec le broutement du cerf. Société de la faune et des parcs du Québec and NSERC–Produits forestiers Anticosti Industrial Research Chair, Quebec City, Quebec. 24 pp.

Potvin, F.; Breton, L.; Gingras, A. 1991. La population de cerfs d'Anticosti en 1988–1989. Direction de la gestion des espèces et des habitats, Ministère du loisir, de la chasse et de la pêche, Quebec City, Quebec. 28 pp.

Potvin, F.; Courtois, R.; Bélanger, L. 1999. Short-term response of wildlife to clear-cutting in Quebec boreal forest: Multiscale effects and management implications. Can. J. For. Res. 29: 1120–1127.

Potvin, F.; Beaupré, P.; Gingras, A.; Pothier, D. 2000. Le cerf et les sapinières de l'île d'Anticosti. Direction de la recherche sur la faune, Société de la faune et des parcs du Québec, Quebec City, Quebec. 35 pp.

Potvin, F.; Beaupré, P.; Laprise, G. 2003. The eradication of balsam fir stands by white-tailed deer on Anticosti Island, Québec: a 150-year process. Ecoscience 10: 487–495.

Prévost, M. 1997. Effects of scarification on seedbed coverage and natural regeneration after a group seed-tree cutting in a black spruce (*Picea mariana*) stand. For. Ecol. Manage. 94: 219–231.

Robbins, C.T.; Mole, S.; Hagerman, A.E.; Hanley, T.A. 1987. Role of tannins in defending plants against ruminants: reduction in dry matter digestion? Ecology 68: 1606–1615.

Rooney, T.P. 2001. Deer impacts on forest ecosystems: a North American perspective. Forestry 74: 201–208.

Rooney, T.P.; Waller, D.M. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. For. Ecol. Manage. 181: 165–176.

Schmitz, O.J.; Sinclair, R.E. 1997. Rethinking the role of deer in forest ecosystem dynamics. Pages 201–223 *in* W.J. McShea, H.B. Underwood, and J.H. Rappole (eds.), The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C.

Sharpe, S. 2002. Forest ecology, forest renewal and introduced species in Haida Gwaii. Science Council of British Columbia, Victoria, B.C. 46 pp.

Sinclair, A.R.E. 1998. Natural regulation of ecosystems in protected areas as ecological baselines. Wildl. Soc. Bull. 26: 399–409.

Stewart, A.J.A. 2001. The impact of deer on lowland woodland invertebrates: a review of the evidence and priorities for future research. Forestry 74: 259–270.

Tilghman, N.G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. J. Wildl. Manage. 53: 524–532.

Vagnoni, D.B.; Garrott, R.A.; Cook, J.G.; White, P.J.; Clayton, M.K. 1996. Urinary allantoin:creatinine ratios as a dietary index for elk. J. Wildl. Manage. 60: 728–734.

Veblen, T.T. 1992. Regeneration dynamics. Pages 152–187 *in* D.C. Glenn-Lewin, R.K. Peet, and T.T. Veblen (eds.), Plant succession: theory and prediction. Chapman & Hall, London, U.K.

Waller, D.M.; Alverson, W.S. 1997. The white-tailed deer: a keystone herbivore. Wildl. Soc. Bull. 25: 217–226.

Westoby, M. 1974. An analysis of diet selection by large generalist herbivores. Am. Nat. 108: 290–304.

Williamson, S.J.; Hirth, D.H. 1985. An evaluation of edge use by white-tailed deer. Wildl. Soc. Bull. 13: 252–257.

Social and natural history of moose introduced to Newfoundland

Brian E. McLaren

Abstract

The island of Newfoundland, 112 000 km² in area, and its moose *Alces alces americana* population form a unique case study of the expansion of an introduced species and its subsequent regulation as a game species. One male moose and one female were introduced to the island from Nova Scotia in 1878, and four adult moose, two females and two males, were successfully introduced to the island from New Brunswick in 1904. Although the motivation to introduce moose was probably to promote export tourism, the species later became fixed in the culture of the province as part of a hunting tradition. Rapid dispersal and low densities characterized the first 25 years of population increase, while wolves *Canis lupus* were extirpated. During population peaks in 1958 and in 1986 and during intermittent and local declines, moose populations have also introduced to Newfoundland increasingly observable, long-term ecosystem effects. This paper surveys some of these topics as a case study on introduced species of social significance.

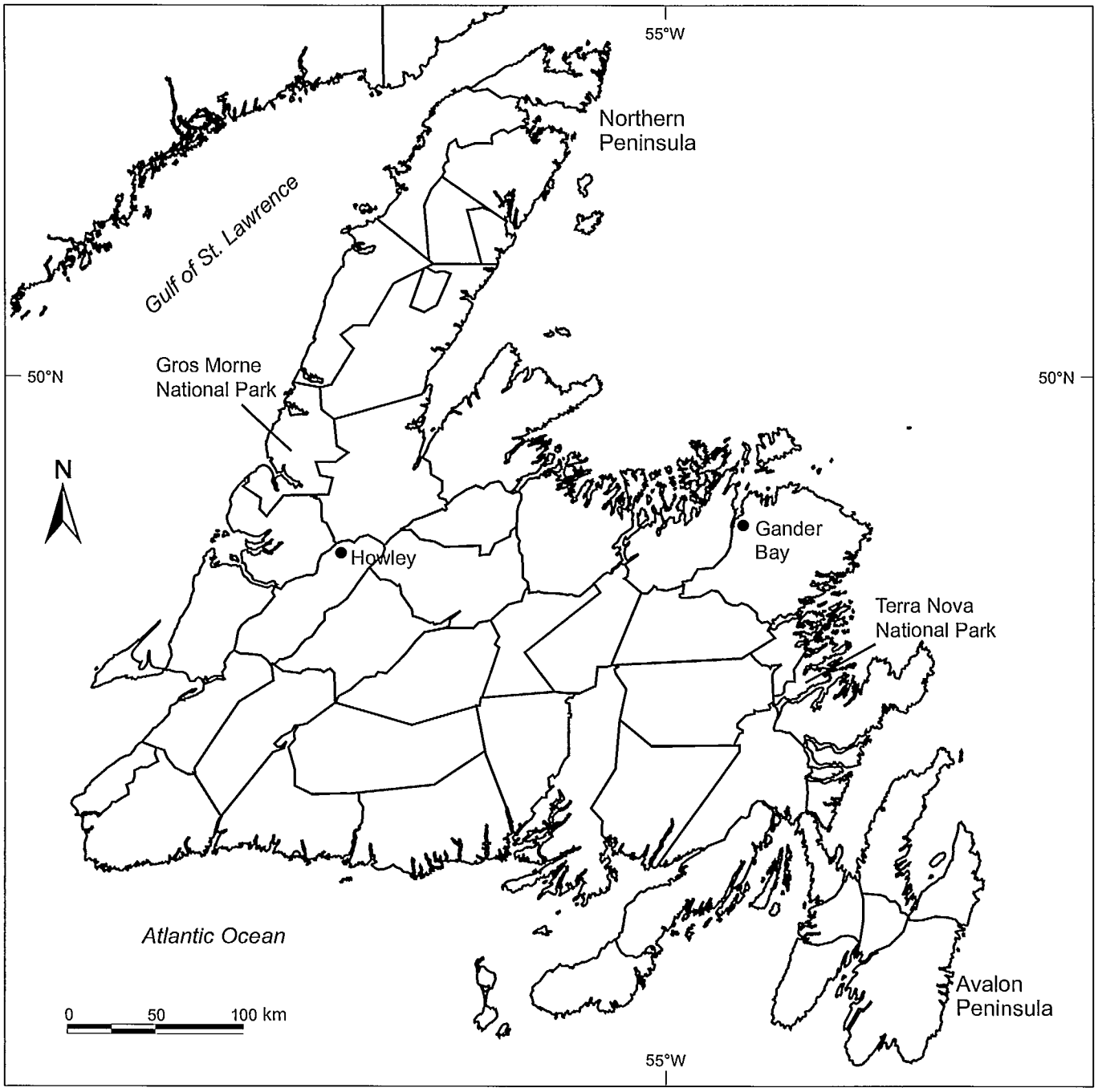
1. Social, economic, and political importance of moose to Newfoundland

Dr. Fred W. Rowe, member of the House of Assembly for Newfoundland in 1951, stated that his motivation to propose and carry out the introduction of moose to St. Lewis Bay on the coast of Labrador was his impression of "the very great need down there for ample supplies of fresh meat during the winter, ... similar [to what] existed in Newfoundland about 50 years before. At that time, in 1904, the Government of the day decided to try out an experiment by introducing moose from the mainland and putting them on the island of Newfoundland. As a result of that experiment, [Rowe's 1953 estimate was that] between 30 000 and 40 000 moose [existed] on the island and [that Newfoundland's] people [were] able to take upwards of 4000 moose every year" (*Moose for Labrador*, Provincial Archives Film, 1953). Rowe obtained his numbers from Wildlife Management Officer Douglas H. Pimlott, occupying a new position whose mandate was that "big game species be managed so as to produce a maximum yield each year ... [in] Newfoundland ... [as] in all areas which import a large portion of their meat requirements" (Pimlott 1957). Pimlott (1959a) drew his own figures from summaries of information provided by resident hunters, encouraged through media such as the Gerald S. Doyle radio broadcast, which stated that "prior to [Pimlott's] study very little detailed information was available on the productivity of moose anywhere in the world." Pimlott (1957) also worked with mailed requests, in which he addressed "Mr Big-Game Hunter: [Y]our assistance is vital to the success of our work, so please assist us, won't you?" The above records form the first documented cases of management of moose as an introduced and vital part of Newfoundland's social ecosystem.

Ironically, the introductions of moose to Newfoundland in 1878 and in 1904 by the government of the day were probably entirely unmotivated by a concern for local meat supply. Beginning in 1869, with the *Act to Amend and Consolidate the Game Laws*, the Newfoundland government documented its support of export tourism, including sport hunting and fishing. Efforts to promote nonresident hunting specifically as a means to pay for new, struggling transportation systems arose in the late 1800s. Following initial railway construction in 1881 with heavy subsidy, the government began to work closely in 1890 with the Reid Newfoundland Company, owner of new steamships and the first contractor for the trans-Newfoundland railway beyond the Avalon Peninsula, to bring tourists to the island. In 1898, the first passenger train ran, and in 1917, the *Newfoundland Quarterly* proudly estimated that 300 tourists had visited the west coast of the island, employing 250 guides. The same publication routinely ran advertisements for the Reid Newfoundland Company, offering "tourists, sportsmen and health-seekers the grandest scenery in the Western Hemisphere ... and finest ... hunting grounds in the world."

John Nowlan of Chatham, New Brunswick, who was raised by the nephew of John Connell, the man responsible for the initial transport (by reins) of moose from the Miramichi area to a steamship destined for Newfoundland, recalled during an interview that he had heard about the capture with payment of "$50 for each moose, a lot of money in those days." Thus, the amount paid as a reward to people who facilitated the transfer of animals to the trains and steamships matched the fee charged by government for nonresident hunting ("excluding Officers of His Majesty's Ships of War") and for "non-domiciled guides." The points for introduction of moose were in central

Figure 1
The island of Newfoundland, where moose were introduced from Nova Scotia in 1878 to Gander Bay and from New Brunswick in 1904 to Howley. Gros Morne National Park, Terra Nova National Park, and the current management area boundaries are illustrated.



Newfoundland (Fig. 1). In 1878, one male and one female were brought to Gander Bay from Nova Scotia, and in 1904, two males and two females to Howley, near Grand Lake, from New Brunswick (Pimlott 1953). These locations were offering tourists government-subsidized lodges or "guest camps that served the sportsman increasingly well by the 1930s" (Smallwood 1994). Moose added nonresident hunting opportunities to the native caribou *Rangifer tarandus terranovae*. Meanwhile, most residents of Newfoundland lived on the coast and would not likely have even seen a moose. The absence of local records of moose during this period (Pimlott 1953) makes it unclear whether they remained at low densities until the 1940s or whether they were just not commonly hunted by residents until that time.

The views were maintained up to the end of the period of colonial government in 1934 that sport fishing and hunting were to be the major attractions for visitors. In 1910, a Game and Inland Fisheries Board was enacted to be responsible for the protection of game, presumably from poaching and overhunting by residents. Licensing of

nonresident hunters and guides provided larger revenue to government than resident hunting fees. During the years of Commission of Government, from 1934 to 1949, British rule had no interest in amending laws pertaining to game management. It was shortly before Confederation with Canada in 1949, when responsibility for fish and game moved to the new Department of Natural Resources and responsibility for tourism moved to the Department of Economic Development, later personally supervised by Premier Joseph R. Smallwood, that views about the importance of resident hunting apparently changed. Coincidentally, the revenues from game licence sales and the overall importance of hunter tourism to the economy were proportionally diminishing in Newfoundland's pre-Confederation years. Developing them further was hardly in the fabric of economic growth envisioned by Smallwood in early post-Confederation years. In 1917, revenue from game licences exceeded $50 000 in a government operating with $5.1 million, accounting for about 1% of total revenues. By 1953, the same figures were reported as $93 700 or about 0.25% of a total government revenue of $37 million.

The earliest efforts in moose management, during 1935–1958, were reported by Douglas Pimlott (1959b), who drew heavily in his approach to managing moose from the experience of his Ph.D. studies at the School of Wildlife Management, University of Wisconsin, and his familiarity with wildlife management in the Fennoscandian countries. Licences were first sold domestically in 1945, and a zoning system was introduced for resident hunters in 1953, when either-sex hunting was also introduced (Fig. 2). By 1960, licence sales were 16 000 with an estimated harvest of 8000, twice what Pimlott had estimated for 1953 (Bergerud 1961). By 1961, the advantage had definitely turned to resident hunters, who could purchase up to three licences, at fees lowered from $10 to $5 in certain areas. This system, in which licences were purchased at local post offices, introduced considerable cheating.

During the 1960s, management of moose became more sophisticated. Pimlott (1953, 1954) had thoroughly questioned and reviewed his mandate of deer introductions to Newfoundland, rationalizing their potential in providing a meat source as well as in damaging forests. He later acknowledged the negative influence of moose on forests as "a problem of considerable economic interest" in Newfoundland (Pimlott 1955, 1963). By 1961, Pimlott had taken a position with the University of Toronto. A new game biologist for Newfoundland, A. Thomas Bergerud, reported Pimlott's problem to the scientific community (Bergerud and Manuel 1968). Bergerud's management program had already begun to include active reduction of moose from some areas of high value to the pulp and paper industry (Bergerud et al. 1968). Bergerud introduced a licence quota system in 1964 in selected areas, when it was recognized that in many other areas the demand for moose was becoming greater than the supply (Mercer and Manuel 1974).

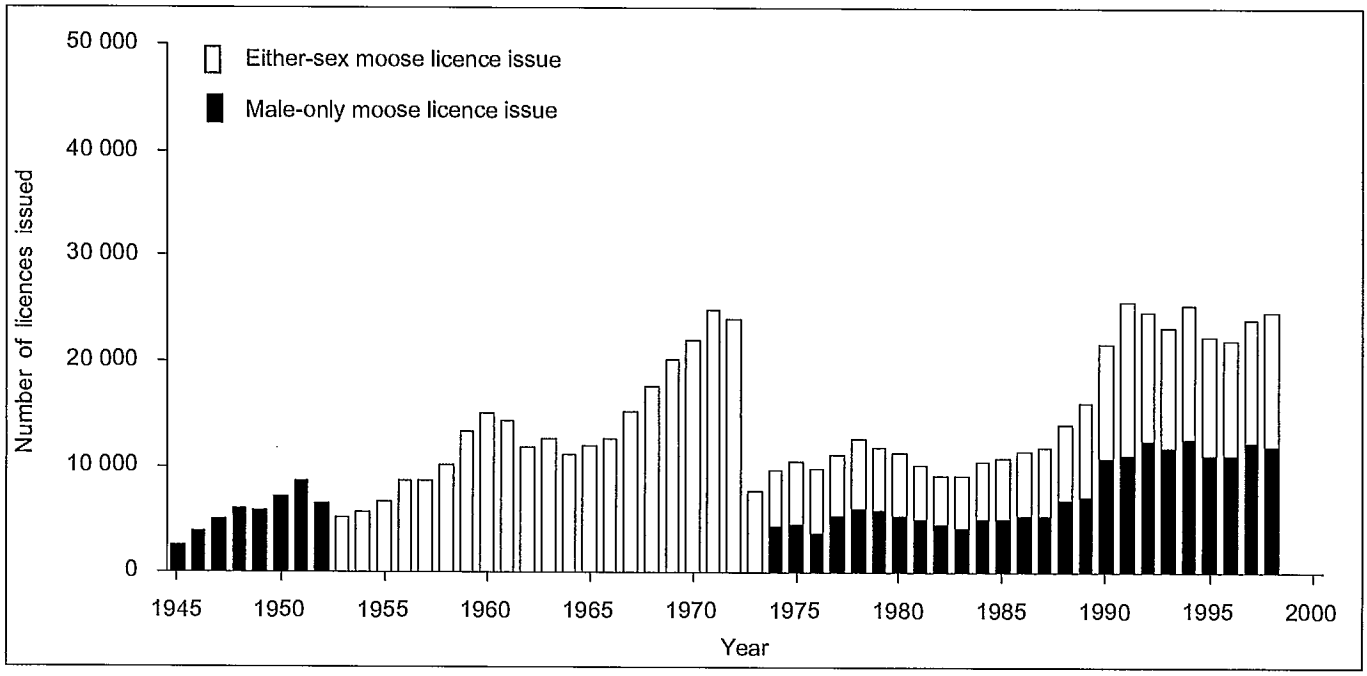
When Thomas Bergerud left the province in 1967, moose management in Newfoundland coincidentally became further complicated by a return of the responsibility for game to the Department of Tourism from the Department of Mines, Agriculture and Resources. The tourism department's new game biologist, W. Eugene Mercer, and subsequent Deputy Minister, Frank Manuel, carefully tracked increasing resident and nonresident licence sales. Nonresident sales increased proportionally between 1953 and 1969 (Fig. 3), with one drop beginning in 1964, when the hunting fee increased for nonresidents from $35 to $75 (Mercer and Manuel 1974). Renewed interest in moose management was also the reaction to a concurrent, general population (and resource) decline from 1960 to 1972. The decline of moose was attributed not only to their overabundance and range deterioration in more remote areas, but also to their overhunting in accessible areas where roads increasingly provided new access to residents (Mercer and Manuel 1974). Accessibility change was surely another motivation to change management approaches, and by 1973 all Newfoundland was managed by area quotas (Fig. 1). With a new computerized draw, 50% fewer licences for moose were sold, and approximately half of these licences were male-only tags (Fig. 2). Hunting became restricted to 36–38 management areas, a few of which closed intermittently.

Other changes to moose management were influenced by a North American sport hunting ethic. Mercer and Strapp (1978) provided a detailed description and justification of these changes for the period 1972–1977. Attempts to refine management further were discussed by Ferguson et al. (1989), when St. John's hosted the 25th North American Moose Conference and Workshop. Mercer and Manuel (1974) implemented the last major changes to management in 1973. Exceptions were during a period in the 1990s, when one response to locally high moose densities was the implementation of "sub-area" management, which included 67 hunting zones at its peak in 1991. A limited sale of calf-only and female-only tags to residents also occurred at this time. Licence issue steadily increased (Fig. 2), undoubtedly as a response to increasing moose populations. The decision to lower licence sales through the 1970s and 1980s was the main reason for the moose population increase (Mercer and McLaren 2002). Hunting season length was gradually extended, beginning in September or October and ending between December and February. By the 1990s, the moose season was 15 weeks long, including a 2-week bow-hunting season. Among these attempts to increase resident hunter opportunities, including greater access to remote areas by some winter hunting, nonresident licence sales were also able to increase. This trend began with a new policy in 1987 (Government of Newfoundland 1987), eventually to have sales reach the accepted allocation of 10% nonresident hunting (Fig. 3). Ultimately, greater interest in outfitting and some public outcry abolished all winter hunting. Subarea management has been all but eliminated in new hunting guidelines.

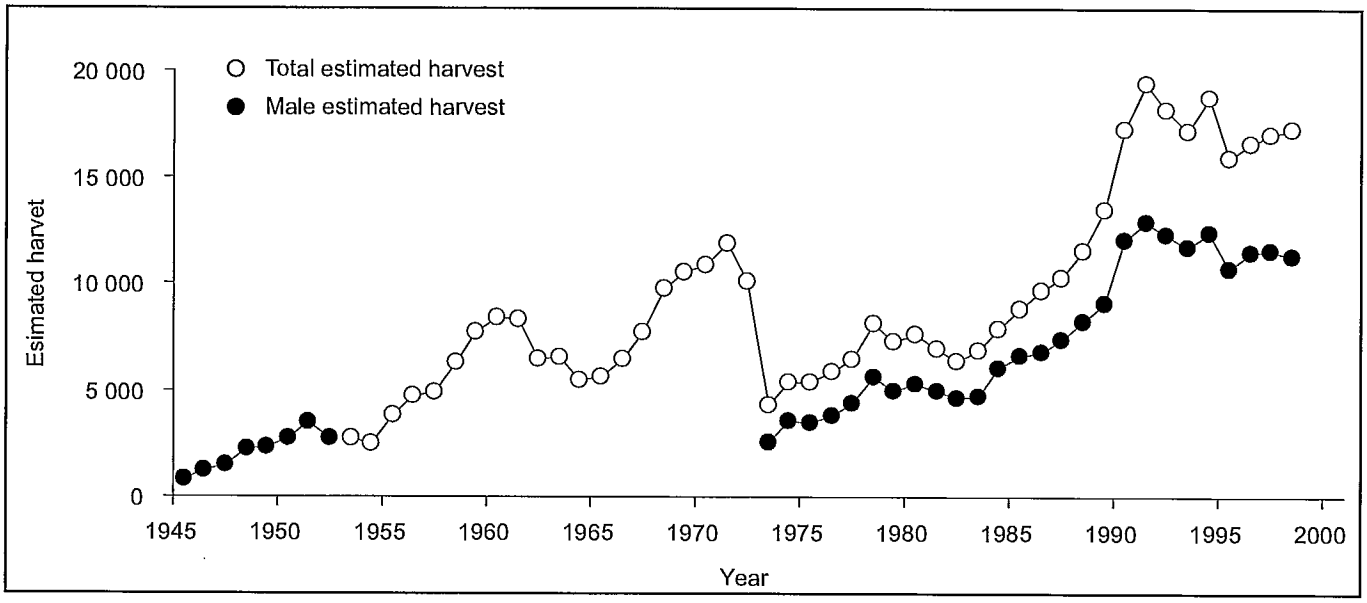
Recently, the province's outfitters and guides have received financial incentives towards new and improved hunting lodges from federal–provincial agreements to subsidize employment and infrastructure for fishers, plant workers, and trawler workers affected by the East Coast marine groundfishery moratorium. Programs included the Atlantic Groundfish Strategy, announced in 1994 as a 5-year, $1.9 billion initiative, and the Atlantic Canada Opportunities Agency, created in 1987, including a Business Development Fund. Outfitters have a strong sociopolitical organization in the form of the Newfoundland and Labrador Outfitters

Figure 2
Trends in moose management for insular Newfoundland, 1945–1998

a) Number of moose licences issued annually. Limited issues of calf-only and female-only licences beginning in 1987 are not included in this figure.



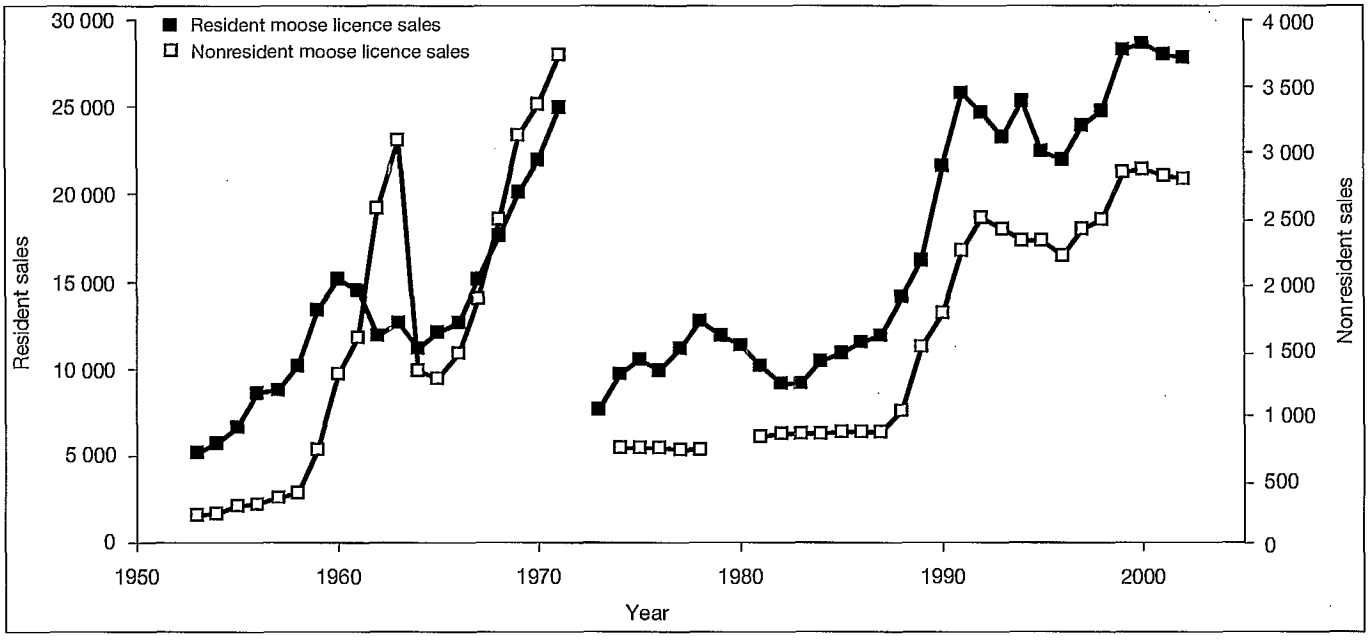
b) Estimated kill from hunter returns



Association. For 2002, 27 820 moose licences were available for sale in insular Newfoundland, with 10% allocated to outfitters for nonresident hunters. The fee for nonresident hunting is now $335, while resident hunting carries a $40 fee.

Political complexity in moose management continues to increase, ironically at the same time that revenue to government from hunting activity continues to diminish in importance. The reasons for this paradox are unclear, but are probably related to the high importance that the people of Newfoundland and Labrador place on traditional activities and on access to the outdoors. In 1997, the Minister responsible for Development and Rural Renewal, Beaton Tulk, who later became Premier, established and led a Cabinet committee for public consultation on the use of outdoor resources. Tulk's report included the recommendation that hunting lodges surrounded by exclusion zones for other camps and remote cottage development continue to allow hunting, fishing, and other activity within the zones. In response to resident concerns

Figure 3
Resident and nonresident moose licence sales during 1953–2002 (from Mercer and Manuel 1974; Government of Newfoundland 1987)



raised in the consultations, however, it was recommended that government review its existing policy with respect to outfitting, with the intention of developing a new and transparent process for approving hunting and fishing lodges (Government of Newfoundland and Labrador 1999). The same minister advised the Inland Fish and Wildlife Division of the Government of Newfoundland and Labrador in 1997 to find "pockets" of moose located during aerial surveys, in which opportunities for temporary nonresident hunting camps could be negotiated. To date, there have been no public reports of these negotiations and recommendations.

The majority of hunting activity in insular Newfoundland is by residents (there are more than 80 000 registered hunters in the province), but outfitters servicing nonresidents still provide government the higher fraction of the revenue from fish and game licence sales, totalling $4.3 million in 2002. Government and the Newfoundland and Labrador Outfitters Association mutually recognize the figure of $40 million as an estimate of the economy involving nonresident hunters, who continue to be attracted to insular Newfoundland by the opportunity of hunting moose, caribou, and black bear *Ursus americana* in combination, making moose hunting difficult to separate economically. This forms 16% of an estimated $250 million tourism industry, but <1% of the total economic activity in the province. Of note, government royalties from fish and game licence sales are today similar to the total revenue from forest management taxes and forestry royalties and fees, largely because forest ownership is on a tenure system including land taxes, but these sales account for <0.2% of provincial revenues and only 0.1% of all government revenue, which is now about $4 billion, including federal transfer payments. Obviously, there is also increasing recognition of a growing economic value associated with nonconsumptive use of moose in promoting tourism, especially as interest in resident hunting wanes with the national trend towards urbanization.

2. Folklore, local ecological knowledge, and social status surrounding moose

After the introduction of moose to Newfoundland, and throughout the period of changing management opportunities that its introduction created, people reacted to what they began to see in their ecosystems with both legend and opinion about this new species. A rich folklore was developed around moose, some around real and some around concocted stories. A unique situation for most of North America, the arrival of moose less than a century ago to Newfoundland means the animal has had little influence on artwork, crests, insignia, or native legend. The following references to folklore and social status of moose, then, might be interpreted more as popular culture.

As musicians in other places around the world have done, Glovertown musicians Buddy Wasisname and The Other Fellers popularized a song that typifies and glorifies the hunting camp with the chorus "Got to Get Me Moose, B'y" (*Greatest Misses*, Third Wave Productions, 2000). The lyrics in this song include a list of the time and expense devoted by people in Newfoundland and Labrador to moose hunting. These costs, today involving hunting by truck and all-terrain vehicle, usually make obtaining moose far more expensive than the current $43 resident licence fee, and such "sport hunting" often substantially exceeds the cost of an equivalent amount of meat purchased (e.g., as beef).

Illustrations associated with people's knowledge about moose gained from hunting or observing them constitute a rich local ecological knowledge about moose behaviour. Local ecological knowledge includes references to calving grounds, mating areas, and winter yards, all locations that are difficult to illustrate using scientific terms or measurements, probably because of natural diversity in these areas, geographic variation (Bubenik 1998), changing

landscapes (McLaren et al. 2000a; Welch et al. 2000), and the fact that they represent atypical moose behaviour (Bubenik 1998; Testa et al. 2000). Indeed, there are only two published scientific papers on moose behaviour in Newfoundland (Dodds 1958, 1959), written during a time when their author was stationed as a field biologist in Cormack and worked closely with Wildlife Officer Robert Folker. Local ecological knowledge also typically includes reference to "black" and "blond" moose, usually in comparing quality of meat (black is superior). This knowledge illustrates astute observation of moose, whose hair coloration differs depending on their diet and age, lighter for older moose feeding in poorer habitats.

Moose continue to get media and political coverage in Newfoundland. The frequency of moose collisions, especially on the Trans-Canada Highway—approximately 600 vehicle accidents involving about two human fatalities per year—leads to much comment. Professional review of moose–vehicle collisions thus has preoccupied both the scientist (Oosenbrug et al. 1986, 1991; Joyce and Mahoney 2001) and the politician (Government of Newfoundland and Labrador 1997) for some time now. Another preoccupation of industry is moose damage to crops, fruit or ornamental trees, and shrubs (Government of Newfoundland and Labrador 2002). Government has made efforts to promote healthy eating, with wild game like moose included in a balanced, low-cholesterol diet (Government of Newfoundland 1986).

3. Population increase, habitat changes, and ecosystem effects

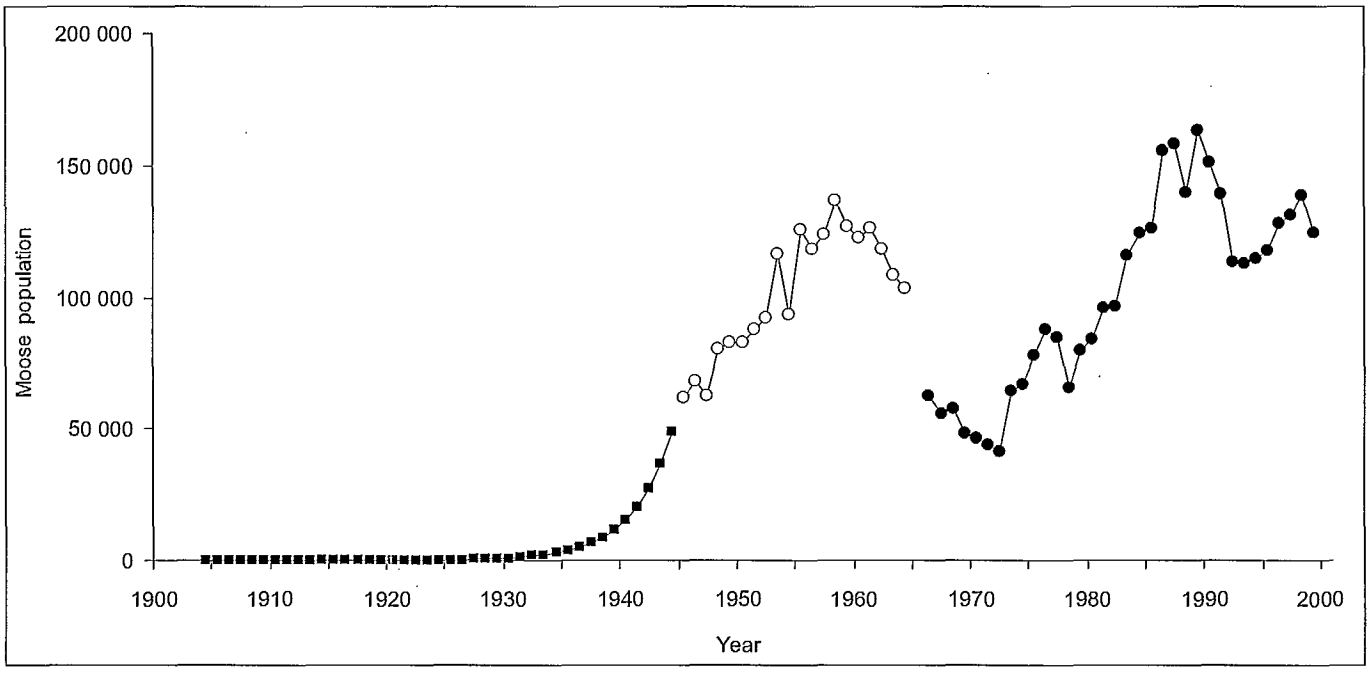
Pimlott (1953) considered the success or failure of the first introduction in 1878 of moose from Nova Scotia unresolved. Several sightings of moose beginning in 1913 in the Gander Bay area (the location of the first introduction), as well as the lack of sightings between Gander Bay and Howley (the location of the second introduction in 1904), made it probable that the first introduction was a success. However, Pimlott (1953) added that the "spread of these [first] moose lacked the dynamic results of the second introduction" and suggested that "large-scale forest fires which swept the eastern section of the island in the 2 or 3 decades following ... [introduction] could have been a factor." More detail on the early distribution and rapid dispersal of moose in Newfoundland following 1904 is found in Pimlott (1953). Genetic information from moose obtained during the past decade (Broders et al. 1999) substantiates Pimlott's (1953) comment about the relative rates of spread of the two introductions. Higher genetic distance of a Newfoundland sample from a Nova Scotian sample than from New Brunswick moose (the source of the second introduction) actually makes the success of the first introduction doubtful. The work by Broders et al. (1999) also shows that because genetic loss occurred with subsequent introduction to the Avalon and Northern peninsulas (Fig. 1), dispersal probably occurred later to these areas.

The period of management from 1935 and particularly 1945 onward is described above with references to Pimlott (1959b), Bergerud (1961), and Mercer and Manuel (1974). Using this information and data provided by hunters, Mercer and McLaren (2002) offered the most recent population reconstruction for moose in Newfoundland (Fig. 4). During 1953–1956, an increase rate (r) was estimated for central Newfoundland at $r = 0.33$, based on observations of young moose in midwinter surveys (Pimlott 1959a). Keith (1983) calculated a North American average intrinsic rate of increase for moose of $r = 0.23$, for situations of unlimited food supply and minimal predation and hunting. Pimlott (1959a) provided a rate that is close to the potential r for moose, because he worked at a time when moose were still expanding in number and range. Mercer and McLaren (2002) described regional situations, where moose populations peaked and remained at habitat carrying capacity, such as in the national parks, where hunting is prohibited, and in less forested areas of Newfoundland that are also less accessible to hunters. There, the average island increase and decline observed since the 1970s (Fig. 4) were not repeated. Hunter-observed population recruitment shows that in such areas, moose density has even exceeded habitat carrying capacity.

Pimlott (1953, 1955) and Dodds (1960) offered the first descriptions of moose habitat and food habits in Newfoundland. These observations were also made in a relatively unexploited range. Pimlott (1963) and Bergerud and Manuel (1968) later described range relationships, making the first references to, and concern for, habitat quality. However, it was not clearly stated that moose were exceeding their carrying capacity in parts of Newfoundland until it was recognized that population decline was occurring generally by the late 1960s. Mercer and Manuel (1974), Albright and Keith (1987), and Ferguson et al. (1989) offered some comment on range deterioration for specific areas of Newfoundland. Defining carrying capacity as the maximum density that can be supported at equilibrium, in a stable environment, and in the absence of time lags, Mercer and McLaren (2002) extrapolated observations of autumn recruitment in an attempt to define carrying capacity generally. Their estimate for Newfoundland boreal forests was 6–9 moose/km^2, calculated from hunter reports of 1.6–2.2 moose seen per day of hunting when a minimum of 20 young/100 adult females was observed.

More detail on home ranges in Newfoundland was provided by radio transmitters on collared moose, used from the late 1980s. Data were available for the first time to confirm habitat associations—for example, that moose in central Newfoundland preferentially occupy specific forest types or that their winter habitat has certain key features, like warmer south-facing slopes where snow depth is less limiting (McLaren et al. 2000a). With documentation of such associations, and with an increasing knowledge about moose diet and plant palatability, measures of carrying capacity calculated simply on the basis of the total availability of twigs (e.g., Parker and Morton 1978) could now be considered overestimates (Mercer and McLaren 2002). In areas with density near carrying capacity, such as in Gros Morne National Park (Fig. 1), collared moose were observed to climb seasonally to higher altitudes as habitat became available with spring snowmelt. Differences in survival in such extreme situations became measurable, from 56% in poor habitat to 72% in better habitat, where black bear predation was a large, but consistent, cause of death in

Figure 4
Moose population trends in insular Newfoundland. For the period 1904–1944 (solid squares), Pimlott's (1959a) observation of increase during 1953–1956 is applied to an exponential function; for the period 1945–1965 (open circles), reports of hunter success are averaged annually; for the period 1966–1999 (solid circles), reports of moose seen by hunters are averaged annually. The axes for the three time series are standardized using the sum of population size estimates across management units surveyed during 1986–1988 and 1996–1998, periods when most of the island was surveyed.



calves observed throughout the park (McLaren et al. 2000b). Such observations lend support to the idea that habitat deterioration might have often affected condition (Ferguson et al. 1989) and density (Mercer and McLaren 2002), in contrast to claims that these have been largely controlled by management decisions (Ferguson and Messier 1996).

Today, moose managers in Newfoundland set a target of 2 moose/km2 of forested area. When a stable population is desired, managers try to match poaching, crippling, and hunting losses to spring recruitment. Management is partly based on estimating the size and age structure of the hunter-killed population by investigating hunter kill and hunter effort (Fryxell et al. 1988; Ferguson and Messier 1996). Attempts to reconstruct population size this way can result in circular arguments (Mercer and McLaren 2002). Lack of precision and inaccuracy in real information about moose density mean that managers typically do not allow for variation in their targets with respect to range or moose condition and, perhaps of greater concern, with respect to biodiversity conservation initiatives.

Moose must be understood in Newfoundland in their context as an introduced species. Before any documented, facilitated introductions, Newfoundland probably had 15 native mammals, including a now-extinct wolf subspecies (*Canis lupus beothucus*). Today, at least 15 mammals have been accidentally or deliberately introduced to this system, increasing the number of mammalian herbivores about threefold. Research to describe moose effects on the ecosystem began by observing changes to plots excluded from moose with fencing (Thompson et al. 1992). Thompson and Curran (1993) added ecological theory to their work when they revisited the sites first investigated by Bergerud and Manuel (1968) to compare site productivity and tree density with herbivore damage 27 years later. Motivation for later collaborative work among pulp and paper companies, the Newfoundland Forest Service, the Wildlife Division of the Department of Tourism, Culture and Youth, Government of Newfoundland and Labrador, and the Canadian Forest Service (Thompson et al. 1989; McLaren et al. 2000b) was for a solution to forestry concerns, often expressed as damage to precommercially thinned balsam fir *Abies balsamea*. Now that moose populations are slightly lower than during the peak years in the 1980s (Fig. 4), such forestry issues are usually relegated to local concerns.

Recent—and important—motivation for study of moose-induced changes to habitat appears to be concern for ecological integrity, usually expressed by Parks Canada. Connor et al. (2000) described changes to plant communities in Gros Morne National Park that could be interpreted as herbivore-caused ecosystem effects. These changes were observed on transects established before moose reached high densities in 1977 and were subsequently monitored in 1996, after closure of hunting created an apparent exponential increase in moose density. Research in Terra Nova National Park (Fig. 1) illustrates that introduced herbivores produce changes in natural vegetation regeneration and ecosystem function not limited to direct moose effects (McLaren et al. 2004). "Invasional meltdown" includes the combined effects of snowshoe hare *Lepus americanus*, red squirrel *Tamiasciurus hudsonicus*, and several introduced gastropods in eliminating germinating plants from disturbed parts of the forest. Thompson and Mallik (1989) made a suggestion

that moose browsing combined with indirect effects from competing vegetation, in their case sheep laurel *Kalmia angustifolia* (and often, in local cases, grasses), could substantially alter eventual tree canopy cover.

The structure, succession, and composition of natural forest communities continue to be altered, in some cases to the extent that their ability to produce moose has been marginalized (Mercer and McLaren 2002), and in others so that sensitive species such as epiphytic lichens or rare plants might be affected (McLaren et al. 2004). Much more needs to be resolved for moose management in Newfoundland and Labrador's island culture and ecosystem. While a beloved and commercially valued animal, as a recognized and dominant introduced species, the moose has created new conservation issues.

Acknowledgements

The preparation of this paper was possible only after many interesting discussions with W.E. Mercer, especially regarding the management history of moose in Newfoundland. The author also acknowledges the Provincial Archives and Legislative Library for help on the paper and the Research Group on Introduced Species for providing funding.

Literature cited

Albright, C.A.; Keith, L.B. 1987. Population dynamics of moose, *Alces alces*, on the south-coast barrens of Newfoundland. Can. Field-Nat.10: 373–387.

Bergerud, A.T. 1961. Ten years of wildlife research in Newfoundland. Proc. Fed. Prov. Wildl. Conf. 25: 17–38.

Bergerud, A.T.; Manuel, F. 1968. Moose damage to balsam fir – white birch forests in central Newfoundland. J. Wildl. Manage. 32: 729–746.

Bergerud, A.T.; Manuel, F.; Whalen, H. 1968. The harvest reduction of a moose population in Newfoundland. J. Wildl. Manage. 32: 722–728.

Broders, H.G.; Mahoney, S.P.; Montevecchi, W.A.; Davidson, W.S. 1999. Population genetic structure and the effect of founder events on the genetic variability of moose, *Alces alces*, in Canada. Mol. Ecol. 8: 1309–1315.

Bubenik, A.B. 1998. Behavior. Pages 173–245 *in* A.W. Franzmann and C.C. Schwartz (eds.), Ecology and management of the North American moose. Smithsonian Institution Press, Washington, D.C.

Connor, K.J.; Ballard, W.B.; Dilworth, T.; Mahoney, S.; Anions, D. 2000. Changes in structure of a boreal forest community following intense herbivory by moose. Alces 36: 111–132.

Dodds, D.G. 1958. Observations of pre-rutting behavior in Newfoundland moose. J. Mammal. 39: 412–416.

Dodds, D.G. 1959. Feeding and growth of a captive moose calf. J. Wildl. Manage. 23: 231–232.

Dodds, D.G. 1960. Food competition and range relationships of moose and snowshoe hare in Newfoundland. J. Wildl. Manage. 24: 522–560.

Ferguson, S.H.; Messier, F. 1996. Can human predation of moose cause population cycles? Alces 32: 149–161.

Ferguson, S.H.; Mercer, W.E.; Oosenbrug, S.M. 1989. The relationship between hunter accessibility and moose condition in Newfoundland. Alces 25: 36–47.

Fryxell, J.M.; Mercer, W.E.; Gellately, R.B. 1988. Population dynamics of Newfoundland moose using cohort analysis. J. Wildl. Manage. 52: 14–21.

Government of Newfoundland. 1986. Provincial hunting guide. Department of Tourism, Culture and Youth, St. John's, Newfoundland.

Government of Newfoundland. 1987. Discussion paper on commercial hunting and fishing camps in the province of Newfoundland. Queen's Printer, St. John's, Newfoundland.

Government of Newfoundland and Labrador. 1999. Protecting the legacy: Report of the Committee on the Use of Outdoor Resources. Vol. 2. Committee recommendations. Department of Forest Resources and Agrifoods, St. John's, Newfoundland. Available at http://www.gov.nf.ca/releases/1999/drr/out-vol2.htm.

Government of Newfoundland and Labrador. 2002. Moose exclusion with ElectroBraid™ fence, 2000–2001. Newfoundland Crop Insurance Agency, Department of Forest Resources and Agrifoods, St. John's, Newfoundland. Available at http://www.electrobraid.com/wildlife/reports/WicksReport2.html.

Joyce, T.L.; Mahoney, S.P. 2001. Spatial and temporal distributions of moose–vehicle collisions in Newfoundland. Wildl. Soc. Bull. 29: 281–291.

Keith, L.B. 1983. Population dynamics of wolves. Pages 66–77 *in* L.N. Carbyn (ed.), Wolves in Canada and Alaska: their status, biology and management. Report Series No. 45, Canadian Wildlife Service, Ottawa, Ontario.

McLaren, B.E.; Mahoney, S.P.; Porter, T.S.; Oosenbrug, S.M. 2000a. Spatial and temporal patterns of use by moose of pre-commercially thinned, naturally-regenerating stands of balsam fir in central Newfoundland. For. Ecol. Manage. 133: 179–196.

McLaren, B.E.; McCarthy, C.; Mahoney, S.P. 2000b. Extreme moose demographics in Gros Morne National Park, Newfoundland. Alces 36: 217–232.

McLaren, B.E.; Roberts, B.A.; Djan-Chékar, N.; Lewis, K.P. 2004. Effects of overabundant moose on the Newfoundland landscape. Alces 40: 45–59.

Mercer, W.E.; Manuel, F. 1974. Some aspects of moose management in Newfoundland. Nat. Can. 101: 657–671.

Mercer, W.E; McLaren, B.E. 2002. Evidence of carrying capacity effects in Newfoundland moose. Alces 38: 123–141.

Mercer, W.E.; Strapp, M. 1978. Moose management in Newfoundland, 1972–1977. Alces 14: 227–246.

Oosenbrug, S.M.; McNeily, R.W.; Mercer, W.E.; Folinsbee, J.F. 1986. Some aspects of moose–vehicle collisions in eastern Newfoundland, 1973–85. Alces 22: 377–394.

Oosenbrug, S.M.; Mercer, W.E.; Ferguson, S.H. 1991. Moose–vehicle collisions in Newfoundland: management considerations for the 1990s. Alces 27: 220–225.

Parker, G.R.; Morton, L.D. 1978. The estimation of winter forage and its use by moose on clearcuts in northcentral Newfoundland. J. Range Manage. 31: 300–304.

Pimlott, D.H. 1953. Newfoundland moose. Trans. N. Am. Wildl. Conf. 18: 563–581.

Pimlott, D.H. 1954. Should white-tailed deer be introduced into Newfoundland? Trans. Fed. Prov. Wildl. Conf. 18: 6–26.

Pimlott, D.H. 1955. Moose and the Newfoundland forests. A report to the Newfoundland Royal Commission on Forestry. Newfoundland Department of Mines and Resources, St. John's, Newfoundland. 26 pp.

Pimlott, D.H. 1957. Moose reproduction study. Preliminary report (unpublished). Wildlife Division, Department of Natural Resources, Government of Newfoundland and Labrador, St. John's, Newfoundland.

Pimlott, D.H. 1959a. Reproduction and productivity of Newfoundland moose. J. Wildl. Manage. 23: 381–401.

Pimlott, D.H. 1959b. Moose harvests in Newfoundland and Fennoscandian countries. Trans. N. Am. Wildl. Conf. 24: 424–448.

Pimlott, D.H. 1963. Influence of deer and moose on boreal forest vegetation in two areas of Eastern Canada. Trans. Int. Union Game Biol. Congr. 6: 105–116.

Smallwood, J.R. 1994. Encyclopaedia of Newfoundland and Labrador. Vol. 5 (Tourism). ISER Publications, Memorial University, St. John's, Newfoundland. 706 pp.

Testa, J.W.; Becker, E.F.; Lee, G.R. 2000. Movements of female moose in relation to birth and death of calves. Alces 36: 155–162.

Thompson, I.D.; Curran, W.J. 1993. A re-examination of moose damage to balsam fir – white birch forests in central Newfoundland: 27 years later. Can. J. For. Res. 23: 1388–1395.

Thompson, I.D.; Mallik, A.U. 1989. Moose browsing and allelopathic effects of *Kalmia angustifolia* on balsam fir regeneration in central Newfoundland. Can. J. For. Res. 19: 524–526.

Thompson, I.D.; McQueen, R.E.; Reichardt, P.B.; Trenholm, D.G.; Curran, W.J. 1989. Factors influencing choice of balsam fir twigs from thinned and unthinned stands by moose. Oecologia 81: 506–509.

Thompson, I.D.; Curran, W.J.; Hancock, J.A.; Butler, C.E. 1992. Influence of moose browsing on successional forest growth on black spruce sites in Newfoundland. For. Ecol. Manage. 47: 29–37.

Welch, I.D.; Rodgers, A.T.; McKinley, R.S. 2000. Timber harvest and calving site fidelity of moose in northwestern Ontario. Alces 36: 93–103.

The Alaska perspective—deer populations in the presence of wolves

Matthew D. Kirchhoff and David K. Person

Abstract

This paper examines the influence of wolves *Canis lupus* on Sitka black-tailed deer *Odocoileus hemionus sitkensis* populations in southeast Alaska, and attempts to predict the effects of introducing wolves to Haida Gwaii (Queen Charlotte Islands, British Columbia) deer populations and their habitat. In general, deer numbers on wolf-free islands are about 40% higher than on islands with wolves. There is high variability, however, with deer being fewest on islands where wolves and black bears *Ursus americanus* are abundant. Wherever deer are abundant in southeast Alaska, the biomass and architecture of understory plants are noticeably affected, as on Haida Gwaii.

In 1960, four wolves were released on Coronation Island (78 km²)—an island with abundant deer but no native predators. Within 5 years, wolf numbers increased to 12, and deer populations plummeted. The wolf population eventually died out, and deer populations rebounded to pre-introduction levels. This experiment confirmed the rapidity with which wolves can reduce a population of deer, and shows that a relatively large geographic area is needed for a stable wolf–deer relationship to become established.

Finally, we modelled the likely response of deer to the hypothetical introduction of wolves on Haida Gwaii, using a 100-year time frame. The model results showed deer declining rapidly at first from 113 000 to 75 000 over the first 12 years after the introduction of wolves. The wolf populations peaked 10 years after introduction and then declined, before stabilizing at about 550 individuals. The vegetation, now released from heavy browsing pressure, began to recover slowly, with K (carrying capacity) increasing about 1% per year. The deer, having access to higher quality forage, became more productive. Their population recovered, "out-producing" the predation loss and stabilizing at about 85 000–90 000 deer.

This paper suggests that, based on experience in Alaska, it is theoretically possible to bring deer, wolves, and native plants into better balance in old-growth temperate rainforests like those on Haida Gwaii. However, it also predicts that deer would remain at high enough population levels to exert a measurable influence on the flora, especially on highly preferred forage species. Collateral damage to other faunal elements would be likely if wolves were to be introduced.

1. Introduction

In southeast Alaska, as on Haida Gwaii (Queen Charlotte Islands, British Columbia), Sitka black-tailed deer *Odocoileus hemionus sitkensis* are abundant and widespread and exert direct or indirect control over many plants and other animals in the ecosystem (Hanley 1993). Two important differences distinguish the natural ecosystems of Haida Gwaii and southeast Alaska: 1) deer are native to the islands of southeast Alaska; and 2) deer coexist with large mammalian predators, including wolves *Canis lupus*, brown bears *Ursus arctos,* and black bears *Ursus americanus*. Understanding how these predator assemblages influence deer populations in southeast Alaska, and the subsequent response of the vegetation can inform debate about different means of reducing deer numbers on Haida Gwaii and restoring the habitat to pre-deer conditions.

The environment of southeast Alaska is similar in many respects to that found on Haida Gwaii (Table 1), so data and ecological relationships from one area are relatively transferable to the other. In Alaska, we have the opportunity to compare deer densities on individual islands with and without wolves (a quasi treatment and control design), as well as to track deer population response to the experimental introduction of wolves on a small predator-free island (a before and after design). We complement these examples with theoretical models that were developed to predict the interactions among deer, wolves, and their habitat in southeast Alaska (Van Ballenberghe and Hanley 1984; Person 2001). We use the Person (2001) model with data from Haida Gwaii to show how deer populations on Haida Gwaii would likely respond to the introduction of wolves.

2. Study area

The Alexander Archipelago of southeast Alaska encompasses 7.6 million hectares of land area, a dozen major islands, each over 75 km², and a narrow strip of adjoining mainland. The archipelago spans 500 km north to south, and 150 km east to west. The southernmost and westernmost islands are strongly influenced by warm maritime air, keeping summers cool and winters relatively wet. Rainfall on the southern islands is high throughout the year, whereas snowfall in winter is light and rarely persistent at sea level.

Table 1
The land area, climate, and large mammal populations on Prince of Wales Island (Game Management Unit 2) in southeast Alaska and Haida Gwaii, British Columbia

	Game Management Unit 2: Alaska (with wolves)	Queen Charlotte Islands (without wolves)
Land area (km²)	9 324	10 000
Deer winter range (km²)[a]	6 154	8 390
Annual precipitation (mm)[b]	2 623	1 321
Mean temperature (°C)[b]	7.6	8.0
Forest type	*Tsuga/Picea/Thuja*	*Tsuga/Picea/Thuja*
Wolves	High	None
Black bears	High	Low
Estimated deer density from pellet group counts on large island[c]	9/km²	13/km²
Estimated deer population from line transects and drives on small islands[d]	n.a.	n.a.
Ecological carrying capacity[e]	105 000	80 000
Reported hunter-killed deer[f]	5 100	881

[a] Assumes one-third of land area is >450 m and not usable by deer in winter due to snow.
[b] Climate data are from Annette Island, Alaska, and Sandspit, B.C., respectively.
[c] Engelstoft (2001) and Kirchhoff and White (2002) (19 watersheds, most recent 2 years).
[d] Martin and Baltzinger (2002).
[e] Person (2001) for Game Management Unit 2, and assumed for British Columbia.
[f] Hicks (2001) and MWLAP (2002).

The southern end of the Alexander Archipelago is only 50 km from Haida Gwaii.

Vegetation throughout the archipelago is typical of the perhumid temperate rainforest type (Alaback 1991, 1995), which corresponds roughly with the Coastal Western Hemlock biogeoclimatic zone (Pojar et al. 1987). Trees occur below 650 m elevation, and are predominantly western hemlock *Tsuga heterophylla*, Sitka spruce *Picea sitchensis*, and, on the southern islands, western redcedar *Thuja plicata*. The shrub layer is dominated by *Vaccinium* spp., false azalea *Menzesia ferruginea*, salal *Gaultheria shallon*, devil's club *Oplopanax horridus*, and salmonberry *Rubus spectablis*. The herb layer includes a variety of forbs (e.g., bunchberry *Cornus canadensis*, five-leaved bramble *Rubus pedatus*, spleenwort-leaved goldthread *Coptis asplenifolia*, false lily-of- the-valley *Maianthemum dilatatum*) and ferns (oak fern *Gymnocarpium dryopteris*, deer fern *Blechnum spicant*, spiny wood fern *Dryopteris dilatata*, and sword fern *Polystichum munitum*). The abundance and variety of individual plant species vary on a fine spatial scale, reflecting discontinuities in canopy cover, soil type, drainage, and browsing by deer (Hanley 1987; Hanley and Hoel 1996; Hanley and Brady 1997).

One of the most intriguing aspects of the Alexander Archipelago is the unique distribution of land mammals found on different islands (Klein 1965a, MacDonald and Cook 1996). The large islands in the northern half of the archipelago have abundant brown bears, but no black bears and no wolves (Fig. 1). Islands in the southern half of the archipelago have black bears and wolves, but no brown bears. All three large predators coexist on the mainland. This distribution is presumably related to colonization patterns following the retreat of glaciers, and subsequent isolation by rising sea levels following the Wisconsin ice age 13 000–15 000 years ago (Klein 1965a). However, recent evidence from fossil remains found in caves indicates that brown bears, and perhaps some other mammals, occupied ice-free coastal refugia continuously over the last 40 000 years (Heaton and Grady 2000, 2003; Heaton 2001).

3. Methods

Direct counts of deer are problematic in any forest environment where they cannot be completely counted from the air or ground. Partial counts may be obtained in alpine areas, along beaches, or with spotlight techniques in open habitats along roads, but because they sample an unknown proportion of the population, they are useful only as trend indicators. An alternate approach is to measure persistent sign left by deer such as trails, tracks, browse utilization, or fecal pellets (Neff 1968; Stordeur 1984; Kirchhoff 1990). Because fecal pellets are persistent, they can be sampled in unbiased and statistically valid ways. With proper design, pellet-group surveys can be used to estimate deer populations (Smith et al. 1969).

Since 1980, the Alaska Department of Fish and Game has annually surveyed deer pellet-group densities on 20–30 watersheds across the archipelago (Kirchhoff and White 2002). In each watershed, three permanent 1-m-wide strip transects extend from the beach to 1375 m elevation (or maximum length 2 km). In watersheds with typical topography, this represents the approximate range available to deer in the winter (Schoen and Kirchhoff 1985). Although these transects sample the range of elevations used by deer in winter, the transect locations themselves are not randomly or systematically placed and therefore may not represent the population in a given watershed (Kirchhoff and Pitcher 1988).

Converting pellet group densities into an actual number of deer gives a result that is more meaningful to the public and makes it possible to relate populations to measures of ecological carrying capacity (Caughley 1976) and hence to calculate deer numbers potentially available for human hunters and natural predators. If it is assumed that sampling effort is distributed to represent the population, pellet group densities can be converted to deer densities with knowledge of 1) the defecation rate, 2) how long pellet groups remain visible, and 3) the accuracy of the count (or how many groups are missed with normal effort). In Alaska, Kirchhoff (1990) determined these values empirically for a known-size population of deer that were transplanted to a small deer-free island (Table 2). Although the exact values vary with weather, habitat type, and crew experience (Kirchhoff and Pitcher 1988), they can nevertheless provide a basis for general comparisons.

Data on defecation rates, group detectability, and persistence of pellet groups are not available from Haida Gwaii, but we assume that conditions are similar enough to justify using the same conversion factor.

Figure 1
The Alexander Archipelago of southeast Alaska, showing the location of wolf-free islands: Admiralty, Baranof, Chichagof, and Coronation. All other large islands, as well as the mainland, have resident wolves.

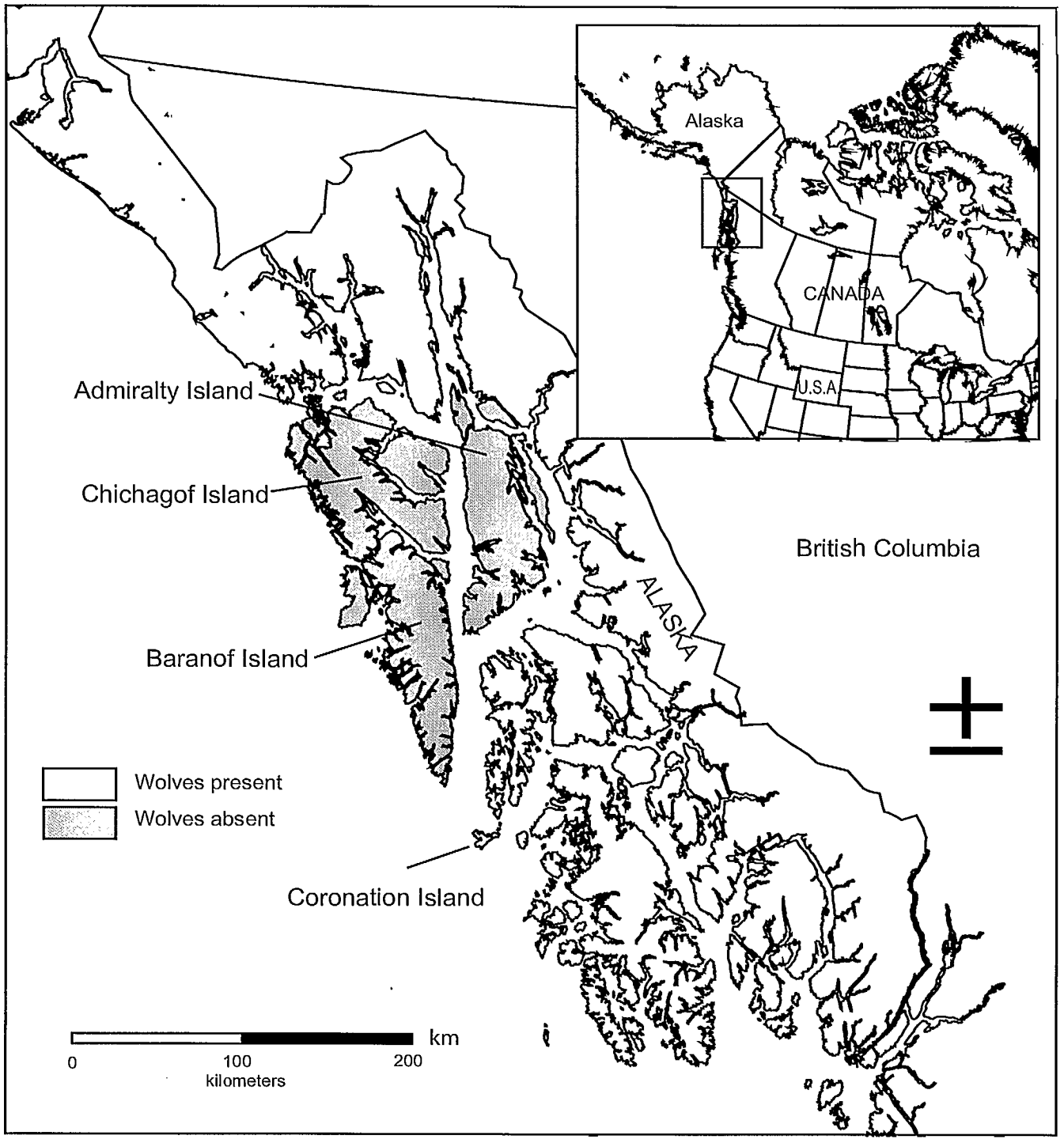


Table 2
Assumptions for the Monte Carlo model simulations. Values for input variables are randomly drawn from data distributions with the specified means and standard deviations. Because the variables are drawn randomly for each simulation, the results of each simulation vary, sometimes markedly. The model results are average results for 500 independent simulations.

Initial deer carrying capacity (K)	80 000
Deer R_{max} (maximum rate of increase)	0.6
Theta	2.0
Predation rate (deer killed/wolf per year)	26
Standard deviation of predation rate	4.0
Mean wolf litter size (no. of pups)	4.5
Standard deviation of wolf litter size	1.0
Chronic mortality of pups	0.5
Standard deviation of chronic mortality	0.33
Dispersal rate of pups	0.5
Standard deviation of dispersal rate	0.33
Mortality among pups that dispersed	0.77
Standard deviation of mortality among pups that dispersed	0.33
% of wolves trapped each year	0.0
% of deer population harvested annually	0.125

4. Observations and modelling

4.1 Deer populations on islands with and without wolves

The Alaska Department of Fish and Game has permanent pellet-group transects in 127 watersheds in southeast Alaska. Certain key watersheds are surveyed annually, whereas others are sampled much less frequently. We summarized the most recent 2 years of data from 21 watersheds in Game Management Unit 2, which has wolves, and compared them with the most recent 2 years of data from 42 watersheds in Game Management Unit 4, which does not have wolves. Deer populations on wolf-free islands averaged 40% higher than deer populations on wolf-occupied islands. While this number gives a general sense of the magnitude of difference, considerable spatial and temporal variability exists.

The highest densities of deer, and the most obvious effects of browsing, are found on the outer coasts of Baranof and Chichagof islands. Here, winter weather is moderated by the warming influence of the offshore Japanese current. Temperatures are mild and snowfall is light. Deer in these areas are limited by the available food, and browsing pressure has had a great impact on the plant life, similar to that described for Haida Gwaii (Pojar et al. 1980; Pojar 1996). The plants most noticeably affected are *Vaccinium* spp., salmonberry, false azalea, and skunk cabbage *Lysichiton americanum*.

Although the presence of wolves typically means low deer numbers, there are some notable exceptions. For example, Zarembo Island (471 km^2) and Heceta Island (186 km^2) in central southeast Alaska have deer numbers as high or higher than some wolf-free areas (Kirchhoff and White 2002). The common thread here seems to be the unusually low black bear numbers on these islands. No one knows why black bear numbers are low, but both islands are heavily logged with many roads, and both receive heavy human use for sport and subsistence deer hunting. Black bear and wolf numbers may be depressed by both legal and illegal killing.

At the other extreme, some islands in southeast Alaska have had exceptionally low numbers of deer for decades, despite mild winters and excellent range conditions. These islands share a reputation for having very high black bear populations in addition to wolves. They also tend to be unlogged, with few roads, reducing the hunting and trapping pressure on the predators. The combination of moderate wolf numbers and high black bear numbers appears capable of holding deer well below carrying capacity for long periods of time. Deer may be especially vulnerable following a series of severe winters (Mech and Karns 1977).

4.2 Island deer populations following an experimental wolf introduction

Coronation Island is a remote, relatively small (78-km^2) island on the western edge of the Alexander Archipelago (Fig. 2) that has no large predators. Deer populations on the island are food-limited, and the deer are significantly smaller than those on wolf-occupied islands (Klein 1965b). Floristic diversity and abundance on Coronation Island has been affected by long-term browsing pressure from deer (Klein 1965b), with vegetative conditions not unlike the most heavily browsed areas on Haida Gwaii.

In 1960, a biologist with the Alaska Department of Fish and Game introduced four wolves to Coronation Island to study wolf–deer interactions at the population level. Deer and wolf populations were monitored through the presence of tracks, scat, and other signs. Vegetation response was monitored on seven 15-m line transects, and with 25 permanent photo plots (Merriam 1968).

4.2.1 Wolf population

From 1960 to 1965, the wolf population increased to approximately 12 animals. As wolves increased, deer populations declined rapidly, and by 1965, it was difficult to locate even a single deer track (Merriam 1968). The scarcity of deer apparently caused strife within the lone pack, and wolves began killing and eating other. In just a few months (August 1965 to February 1966), the wolf population declined from 12 animals to 3. By August 1966, only two or three wolves were found on the island, and no denning activity was noted. In January 1968, only one wolf remained (Merriam 1968). That lone wolf occupied the island until 1971, when it was killed (Merriam 1971). The island has remained predator-free since.

4.2.2 Wolf diet

Food items occurring in wolf scats parallel these population changes. From 1960–1965, deer were the major food item, although harbor seals *Phoca vitulina* comprised a significant percentage (Fig. 3). As the deer population declined, wolves increased consumption of small, less conventional food items, including birds and shellfish

Figure 2
Coronation Island is a 35-km² island in southeast Alaska with abundant deer populations and no wolves. It was the site of an experimental wolf introduction in 1960.

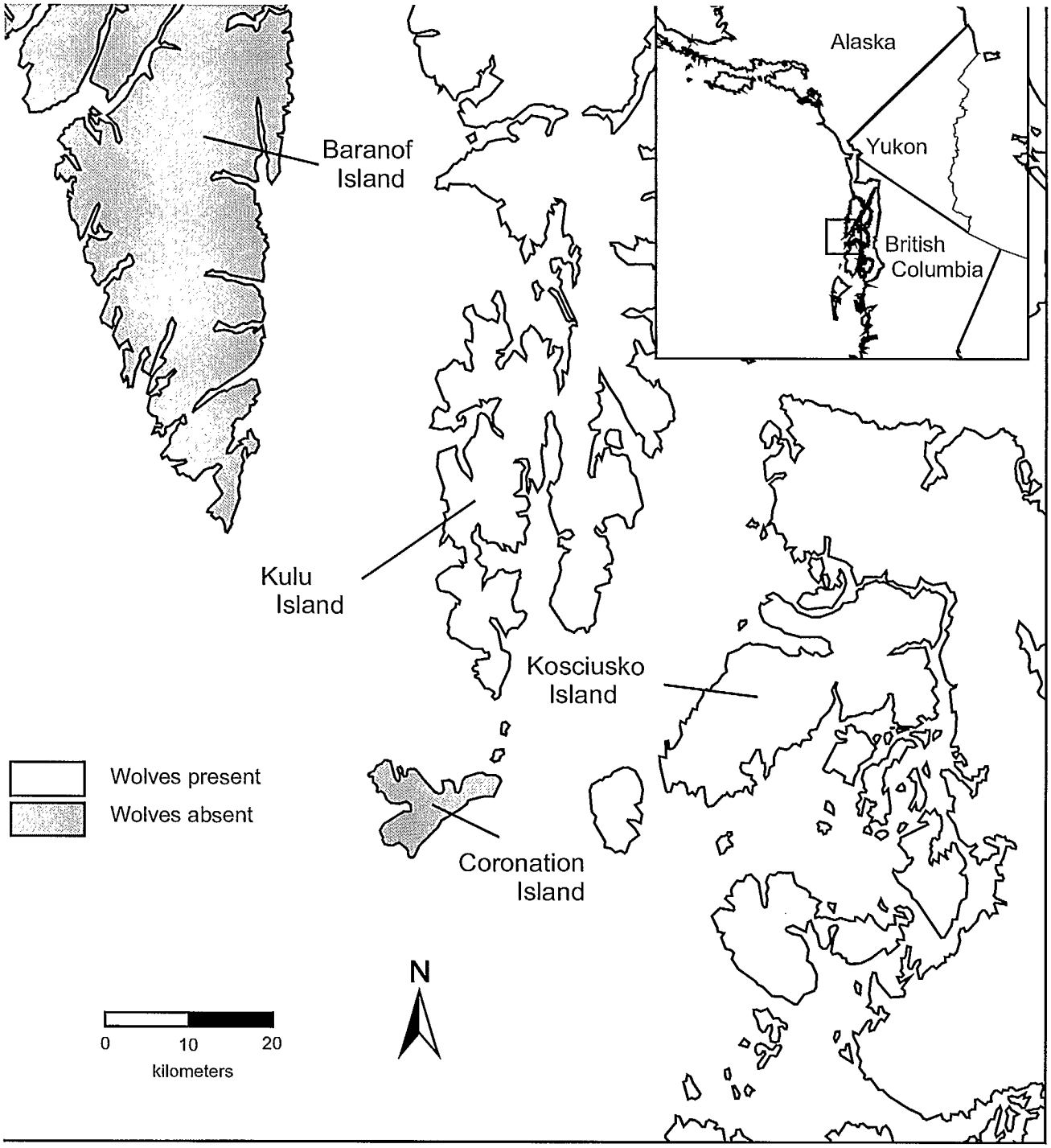
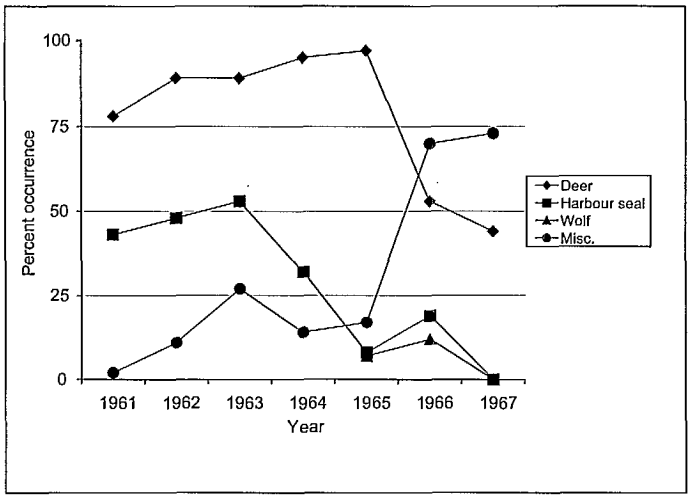


Figure 3
Frequency of occurrence of different food items in the scats of introduced wolves on Coronation Island, 1961–1967 (from Merriam 1968)



scavenged along the intertidal zone. In February 1966, six scats contained only wolf material, and much blood was found along one wolf trail (Merriam 1968). In August, 1966, only seven scats could be located, and one of these contained wolf hair. The lone wolf that occupied the island after 1968 was frequently seen scavenging on the beaches.

4.2.3 Deer population

With only a single wolf on the island, the deer population showed no apparent increase from 1968 to 1971 (Merriam 1971). Whether deer were completely eliminated from Coronation Island is unknown. If they were eliminated, the islands were recolonized soon after wolves disappeared. We consider it more likely that a few individual deer were able to persist throughout the wolf years and their population recovered rapidly once the last wolf was eliminated. Today, the deer population has returned to its original numbers.

4.2.4 Vegetation

In 1960 it was difficult to find an oval-leaved blueberry *Vaccinium ovaliflium* or red huckleberry *V. parvifolium* on the island, and those that were there had grown beyond deers' reach, or were perched in inaccessible locations (Merriam 1968). As deer declined, however, the vegetation responded quite rapidly. Between 1963 and 1965, when deer became scarce, plant occurrence on seven 15-m line transects increased 65% (Merriam 1968). Most of the increase in plant cover was from forbs, and establishment of new *Vaccinium* plants was slower than anticipated. New shrubs were filling in the voids slowly, but lineal growth on the small plants was limited. In contrast, new shoot growth from the base of older *Vaccinium* plants was rapid, with up to 30 cm of new growth observed annually (Merriam 1968).

4.3 Deer populations on Haida Gwaii following the hypothetical introduction of wolves—a model.

Although there has been no formal discussion of wolf introductions in Haida Gwaii, that course is one possible means of controlling deer and helping restore natural vegetation on the Islands. As significant as the ecological ramifications of a wolf introduction might be, we appreciate the important cultural, social, political, and philosophical issues it raises. We are not advocating for a wolf introduction in this paper. However, natural predation offers a possible means of reducing deer numbers with far greater efficiency and effect than hunting can. For that reason, it is worth exploring, through modelling, what the likely response of deer and vegetation might be to a wolf introduction.

Van Ballenberghe and Hanley (1984) modelled how black-tailed deer numbers might respond to wolf predation in the face of changing habitat conditions in southeast Alaska. They concluded that declining habitat quality following logging would make deer less resilient to wolf predation and possibly lead to protracted lows in the deer population cycle. Any factors that increased deer mortality, such as deep persistent snow, poor body condition, or increased mortality due to hunting and predation, deepened and lengthened the lows in the deer population cycle.

Eberhardt (1998) and Person et al. (2001) developed more detailed models that incorporated the functional response of wolves to changes in prey density. Person (2001) incorporated empirical data from his wolf studies on Prince of Wales Island and included stochastic events such as severe winters and fluctuations in the productivity and survivorship of deer and wolves. Results reflected the average outcome over thousands of Monte Carlo simulations. In this paper, we use the Person's (2001) model to predict the likely response of deer on Haida Gwaii to the introduction of wolves.

4.3.1 Model assumptions

The model assumes that three packs of three wolves each are released at widely separated places on the archipelago at year 15 of the simulation. It assumes an average pack size of seven, with a single breeding pair producing a single litter annually averaging 4.5 pups. Pups that stay resident suffer a 50% natural mortality rate; pups that disperse suffer a 70% natural mortality rate (Person 2001). Pack growth and territories are established with social factors constraining wolf density and home range size. There is sufficient land area on the islands to support 30 wolf packs, and there is no hunting or trapping season on these wolves.

Based on surveys of fecal pellet-groups, deer density in forested habitat on Prince of Wales Island is estimated at 9 deer per km^2 (data in Kirchhoff and White 2002); and density on Graham Island has been estimated at 13 deer per km^2 (Englestoft 2001). From line transects counts and deer drives, Martin and Baltzinger (2002) report deer densities of 30 deer per km^2 on several small islands in Haida Gwaii. Based on our experience in southeast Alaska, deer densities on small islands are considerably higher than they are on large islands, and we assume a similar pattern exists

on Hadia Gwaii. Thus, we used the 13 deer per km^2 estimate as the basis for our modelling exercise. When extrapolated to overall suitable habitat on Haida Gwaii, the total population is estimated at 113 000 deer.

Because deer are currently limited by the carrying capacity of the habitat and not by predators or hunting, the model sets ecological carrying capacity (K) at 110 000. Wolves are allowed to expand to a maximum of 31 packs, based on average pack home range size on Prince of Wales Island. As wolves drive deer populations below K, and browsing pressure is reduced, deer forage should increase. The annual increase in K is equal to 5% of the difference between current K and the current deer population. For example, if K is 100 000, and deer populations are 80 000, 5 percent of the difference is 1000, raising K for the next year to 101 000. As deer browsing is reduced, K can potentially increase to a maximum K of 220 000 (2 times present-day K).

The maximum per capita rate of population growth (R_{max}) is determined by age of first reproduction, pregnancy rates, and number of fetuses per pregnant doe. From the literature, we assign maximum rate of growth (R_{max}) for *Odocoileus* spp. at 0.6 (McCullough 1987), and the shape of the net recruitment curve (theta) as 2 (Person 2001; Person et al. 2001). At present, 880 deer (primarily bucks) are harvested annually on Haida Gwaii (reported harvest only), or 0.8% of the population. That same proportion of the projected deer population continues to be harvested annually throughout the simulation. The model can add severe winters at random intervals, with corresponding declines in deer, but for our simulations that feature was turned off.

4.3.2 Model predictions

Monte Carlo simulations ($N = 500$) of our model for Haida Gwaii, with the above input variable, shows that after wolves enter the system, their numbers increase rapidly, peaking at over 700 wolves within 15 years of their introduction. They decline slightly after this peak, stabilizing at a population of 575–600 animals. Deer, as expected, decline with the introduction of wolves, from an initial population of 113 000, to a low of approximately 75 000 animals in year 37 of the simulation (12 years after the wolf introduction). As soon as deer fall below K (110 000), however, the vegetation starts to recover. At year 37, the vegetation is recovering at a rate of 2–3% per year.

One of the significant results of this simulation is the prediction that deer will not decline to extremely low levels with the introduction of wolves. This is due to the fact that once the vegetation is released from intensive browsing pressure, the per capita availability of forage increases, as does the average quality of the diet. This translates into increased productivity (i.e., annual recruitment) of the deer herd. As the carrying capacity of the range continues to rebuild, and deer become more productive, a steady-state equilibrium is established between deer and wolves. Deer do not regain their current population levels over the course of the simulation, but they do remain relatively abundant, stabilizing at between 85 000 and 90 000 deer. Because the deer population stays fairly abundant, the rate at which the vegetation recovers is slowed to about 1% per year and continues at this rate throughout the simulation.

5. Discussion

5.1 Possible outcome of wolf introduction for deer and vegetation

If the objective of a wolf transplant is to reduce the effects of deer on the forest vegetation, the model predicts modest long-term success. Vegetation recovered slowly, but steadily. Given sufficient time it would presumably approximate forest conditions similar to those found on on Prince of Wales Island, Alaska. However, restoring carrying capacity and restoring the original flora of Haida Gwaii are different goals. The vegetation might regain more of a "jungle-like" appearance noted in early accounts (e.g., Hopkinson 1931), but because deer are still abundant on the islands, favoured forbs and shrubs such as skunk cabbage, and salmonberry would probably still be rare. And grazing pressure on western redcedar seedlings will be significantly lessened but not eliminated.

The effects of wolves on deer, and of deer on vegetation would not be uniformly felt across the archipelago. Wolves occupy relatively large home ranges compared with deer, and the smaller and more remote the island, the less likely it is to be used by wolves (Kirchhoff 1994). We would expect remote islands, such as Reef, to be infrequently visited by wolves and remain overbrowsed. The larger, more contiguous islands would realize the greatest benefits from a wolf introduction. If the Alaskan experience on Coronation Island is any guide, wolves released on smaller, remote islands (e.g., with <3 000 deer) would not persist. They would either move to larger islands if the distance is short enough (e.g., <5 km) or die from lack of food after the deer were depleted.

The projected deer population could continue to sustain intense hunting without effect. However, the increase in understory vegetation might make hunting more difficult. Deer may also avoid open roadsides and other open habitats if these areas expose deer to increased predation pressure by wolves. On the other hand, if wolves were trapped and hunted by humans, they probably would avoid heavily used roads and human settlements (Person 2001). This security from predators may draw more deer into these "safe" zones, and increase availability and success for hunters.

5.2 Driving factors

Whether the deer population stabilizes at low or high levels is governed by several key factors. For deer to remain abundant, net ecological carrying capacity must increase. We assumed that if every deer were to be instantly removed from the islands, K would increase by 5% a year to an ecological maximum that is triple what we see today. Although that rate of ecological "repair" is not based on hard data, it is clear from the Coronation experiment that the vegetation responds quite rapidly when released from browsing pressure (Merriam 1968). Ongoing studies of vegetation response within deer exclosures and on deer cull islands (e.g., Sharpe 2002) should provide an empirical basis for these assumptions in future modelling.

It is important to simultaneously consider a complicating factor, and that is the effects of secondary forest

succession on *K*. The extensive history of clearcut logging on Haida Gwaii means that many former old-growth stands with once-productive understories will grow into even-aged second-growth forests with much lower forage biomass (Alaback 1982). The gradual loss of this productivity cannot be easily regained, no matter what the situation with deer.

On southern Kuiu Island in southeast Alaska, where black bears and wolves are abundant, deer numbers have been extremely low for over 20 years (Kirchhoff and White 2002). Wolves have maintained high numbers because of the availability of alternative prey, such as beaver, salmon, and black bears (L. Peacock, unpubl. data). On Haida Gwaii, alternative prey are likely to be other introduced mammals, such as elk *Cervus elaphus*, beaver *Castor canadensis*, muskrat *Ondatra zibethicus*, and raccoon *Procyon lotor*. In addition to these nonindigenous animals, wolves would also prey on Queen Charlotte Islands black bear *Urus americanus carlottae*, spawning salmon, intertidal marine organisms, and birds. Potential predation on important colonies of ground-nesting ancient murrelets *Synthliboramphus antiquus* would warrant special concern.

6. Conclusions

Evidence from southeast Alaska and elsewhere clearly supports the notion that deer can be kept below the ecological carrying capacity of their range by naturally regulated wolf populations (Mech and Karns 1977; Nelson and Mech 1981; Smith et al. 1987; Janz 1989). Empirical data from selected islands show that it is possible for deer and wolves to coexist at a relatively high equilibrium, but additive mortality from other predators, hunting, or severe winters can also depress deer to low levels for long periods. Simulation models that introduce wolves to Haida Gwaii indicate that a high-level equilibrium is likely. That conclusion assumes that additive mortality from other predators, such as black bears and humans remains low and that vegetation responds quickly once released from heavy browsing pressure.

Understory biomass would likely be restored, but preferred plant species would continue to be underrepresented relative to pre-deer conditions. Adding wolves to Haida Gwaii would certainly reduce deer in the short term, and help restore some of the missing understory, but as history shows, it is the unanticipated consequences of such introductions that prove problematic. Even if scientists were 95% certain that introducing wolves would improve floristic diversity on Haida Gwaii, other societal and ecological ramifications that would have to be considered before such a significant step were taken.

Acknowledgements

We would like to thank K. White, A. Russel, and C. Englestoft for helpful review comments on this manuscript. This work was supported by Federal Aid in Wildlife Restoration Grant W-33-1, job 2.12.

Literature cited

Alaback, P.B. 1982. Dynamics of understory biomass in Sitka spruce – western hemlock forests of southeast Alaska. Ecology 63: 1932–1948.

Alaback, P.B. 1991. Comparative ecology of temperate rainforests of the Americas along analogous climatic gradients. Rev. Chil. Hist. Nat. 64: 399–412.

Alaback, P.B. 1995. Biodiversity patterns in relation to climate and a genetic base for the rainforests of the west coast of North America. Pages 105–133 *in* R. Lawford, P.B. Alaback, and E.R. Fuentes (eds.), High-latitude rainforests of the west coast of the Americas: Climate, hydrology, ecology, and conservation. Springer-Verlag, Berlin.

Caughley, G. 1976. Wildlife management and the dynamics of ungulate populations. Adv. Appl. Biol. 1: 183–247.

Eberhardt, L.L. 1998. Applying difference equations to wolf predation. Can. J. Zool. 76: 380–386.

Engelstoft, C. 2001. Effects of Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) on understory in old-growth forest on Haida Gwaii (Queen Charlotte Islands), British Columbia. M.Sc. thesis, University of Victoria, Victoria, B.C. 113 pp.

Hanley, T.A. 1987. Physical and chemical response of understory vegetation to deer use in southeastern Alaska. Can. J. For. Res. 17: 195–199.

Hanley, T.A. 1993. Balancing economic development, biological conservation, and human culture: the Sitka black-tailed deer *Odocoileus hemionus sitkensis* as an ecological indicator. Biol. Conserv. 66: 61–67.

Hanley, T.A.; Brady, W.W. 1997. Understory species composition and production in old-growth western hemlock – Sitka spruce forests in southeastern Alaska. Can. J. Bot. 75: 574–580.

Hanley, T.A.; Hoel, T. 1996. Species composition of old-growth and riparian Sitka spruce – western hemlock forests in southeastern Alaska. Can. J. For. Res. 26: 1703–1708.

Heaton, T.H. 2001. Late Pleistocene and Holocene vertebrates from the southeast Alaskan mainland. J. Vertebr. Paleontol. 21(3): 59A–60A.

Heaton, T.H.; Grady, F. 2000. Vertebrate biogeography, climate change, and Ice Age coastal refugia in southeastern Alaska. J. Vertebr. Paleontol. 20: 48A.

Heaton, T. H.; Grady, F. 2003. The Late Wisconsin vertebrate history of Prince of Wales Island, Southeast Alaska. Pages 17–53) *in* B.W. Schubert, J.I. Mead, and R.W. Graham, (eds.), Ice age cave faunas of North America. Indiana University Press, Bloomington, Indiana.

Hicks, M. 2001. Deer. Federal Aid in Wildlife Restoration, Survey and Inventory Management Report, Grants W-27-2 and W-27-3, Study 2.0, Alaska Department of Fish and Game, Division Wildlife Conservation, Juneau, Alaska 108 pp.

Hopkinson, A.D. 1931. A visit to the Queen Charlotte Islands. Empire For. 10: 20–36.

Janz, D. 1989. Wolf–deer interactions on Vancouver Island—A review. Pages 26–42 *in* Wolf–prey dynamics and management. Proceedings of a symposium held 10–11 May 1988. Working Report No. WR-40, Wildlife Branch, B.C. Ministry of Environment, Victoria, B.C.

Kirchhoff, M.D. 1990. Evaluation of methods for assessing deer population trends in southeast Alaska. Federal Aid in Wildlife Restoration Final Research Report W-23-3, Alaska Department of Fish and Game, Douglas, Alaska. 35 pp.

Kirchhoff, M.D. 1994. Effects of habitat fragmentation on deer in southeast Alaska. Federal Aid in Wildlife Restoration Final Research Report W-23-3,4,5, W-24-1,2, Study 2.10, Alaska Department of Fish and Game, Douglas, Alaska. 60 pp.

Kirchhoff, M.D.; Pitcher, K.W. 1988. Deer pellet-group surveys in southeast Alaska 1981–87. Federal Aid in Wildlife Restoration Final Report, Job 2.9, W-22-6, W-23-1, Alaska Department of Fish and Game, Douglas, Alaska. 113 pp.

Kirchhoff, M. D.; White, K. 2002. Deer pellet-group surveys in southeast Alaska—2001 report. Alaska Department of Fish and Game, Douglas, Alaska.

Klein, D.R. 1965a. Postglacial distribution patterns of mammals in the southern coastal regions of Alaska. Arctic 10: 7–20.

Klein, D.R. 1965b. Ecology of deer range in Alaska. Ecol. Monogr. 35: 259–284.

MacDonald, S.O.; Cook, J.A. 1996. The land mammal fauna of southeast Alaska. Can Field-Nat. 110: 571–599.

Martin, J.-L. and C. Balzinger. 2002. Interaction among deer browsing, hunting, and tree regeneration. Can. J. For. Res. 32: 1254–1264.

McCullough, D.R. 1987. The theory and management of *Odocoileus* populations. Pages 535–549 *in* C.M. Wemmer (ed.), Biology and management of the Cervidae. Smithsonian Institution Press, Washington, D.C.

Mech, L.D.; Karns, P.D. 1977. Role of the wolf in a deer decline in the Superior National Forest. Research Report NC-148, North Central Forest Service, U.S. Department of Agriculture, St. Paul, Minnesota.

Merriam, H.R. 1968. Deer report. Federal Aid in Wildlife Restoration Report. W-15-R-2 and 3, Alaska Department of Fish and Game, Douglas, Alaska. 30 pp.

Merriam, H. R. 1971. Deer report. Federal Aid in Wildlife Restoration Report. 17-2 and 3, Alaska Department of Fish and Game, Douglas, Alaska. 6 pp.

MWLAP 2002. Big game hunting statistics for the 2001/02 season. Fish and Wildlife Recreation and Allocation Branch, B.C. Ministry of Water, Land and Air Protection, Victoria. 112 pp.

Neff, D.J. 1968. The pellet-group count technique for big game trend, census, and distribution: a review. J. Wildl. Manage. 32: 597–614.

Nelson, M.E.; Mech, L.D. 1981. Deer social organization and wolf predation in northeastern Minnesota. Wildl. Monogr. 77: 1–53.

Person, D.K. 2001. Alexander Archipelago wolves: ecology and population viability in a disturbed, insular landscape. Ph.D. thesis, University of Alaska, Fairbanks, Alaska. 174 pp.

Person, D.K.; Bowyer, R.T.; Van Ballenberghe, V. 2001. Density-dependence of prey and functional responses of wolves: interpreting predator–prey ratios. Alces 37(2):253–273.

Pojar, J. 1996. The effects of deer browsing on the plant life of Haida Gwaii. Pages 90–98 *in* G.G. Wiggins (ed.), Proceedings of the cedar symposium: growing western redcedar and yellow-cypress on the Queen Charlotte Islands/Haida Gwaii. B.C. Ministry of Forests / Canada – British Columbia South Moresby Forest Replacement Account, Victoria, B.C.

Pojar, J.; Lewis, J.T.; Roemer, H.; Wilford, D.J. 1980. Relationships between introduced black-tailed deer and the plant life of the Queen Charlotte Islands, British Columbia. Unpublished report, B.C. Ministry of Forests, Smithers, B.C. 63 pp.

Pojar, J.; Klinka, K.; Meidinger, D.V. 1987. Biogeoclimatic ecosystem classification in British Columbia. For. Ecol. Manage. 22: 119–154.

Schoen, J.W.; Kirchhoff, M.D. 1985. Seasonal distribution and home range patterns of Sitka black-tailed deer on Admiralty Island, southeast Alaska. J. Wildl. Manage. 49: 96–103.

Sharpe, S. 2002. Forest ecology, forest renewal, and introduced species in Haida Gwaii—final report. Reference PA97335-BRE, Forest Renewal B.C. Program, Science Council of British Columbia. 38 pp.

Smith, C.A.; Young, E.L.; Land, C.R.; Bovee, K.P. 1987. Predator-induced limitations on deer population growth in southeast Alaska. Federal Aid in Wildlife Restoration Project W-22-4,5,6, Job 14.14, Alaska Department of Fish and Game, Douglas, Alaska. 20 pp.

Smith, R.H.; Neff, D.H.; McCulloch, C.Y. 1969. A model for the installation and use of a deer pellet-group survey. Special Report No. 1, Federal Aid in Wildlife Restoration Report W-78-R, Arizona Game and Fish Department, Phoenix, Arizona. 30 pp.

Stordeur, L.A. (ed.). 1984. Proceedings of a seminar on ungulate pellet-group sampling and data analysis techniques. Report WH-7, Research Branch, B.C. Ministry of Forests Victoria, B.C. 98 pp.

Van Ballenberghe, V.; Hanley, T.A. 1984. Predation on deer in relation to old-growth forest management in southeastern Alaska. Pages 291–296 *in* W.R. Meehan, T.R. Merrell, Jr., and T.A. Hanley (eds.), Fish and wildlife relationships in old-growth forests: Proceedings of a symposium held in Juneau, Alaska, 12–15 April 1982. American Institute of Fishery Research Biologists, Morehead City, North Carolina.

Conclusions

Caption:
Top: Gradient of images going from the interior to the shoreline on an island without deer
Bottom: Gradient of images going from the interior to the shoreline on an island with deer for over 50 years
Credits:
All except deer photo: RGIS, Jean-Louis Martin
Deer photo: RGIS, Sylvie Blangy

Deer and biodiversity on Haida Gwaii: lessons, questions, and decisions

Jean-Louis Martin, Anthony J. Gaston, Todd Golumbia, and Sean Sharpe

Abstract

In the presence of the introduced Sitka black-tailed deer *Odocoileus hemionus sitkensis*, plant diversity in Haida Gwaii (Queen Charlotte Islands, British Columbia) is much reduced, the reduction being greatest on islands with the longest history of deer browsing. The reduction in plant abundance and diversity is correlated with a reduction in insect abundance and songbird abundance and diversity. A web of effects and interactions links deer, nest predators, and songbird reproductive success, suggesting that the arrival of deer has initiated a cascade of effects, flowing down to primary producers and bouncing back to insects and birds. The introduction has imposed a heavy cost on the biodiversity of Haida Gwaii: although the list of species found in the Islands has changed little, their relative abundance has changed enormously. Not only do these changes affect the functioning of the local ecosystems, but, by threatening unique island genotypes, they constitute a threat to global biodiversity. Our results contribute convincing arguments to those who wish to preserve healthy predator populations, showing that without predators, deer populations pose a threat to all components of forest ecosystems.

1. Theoretical background

As emphasized by Schmitz and Saint-Clair (1997), "ecologists often conceptualise natural ecosystems as having three interacting components: (1) primary producers (plant trophic level) that convert sunlight and nutrients from biochemical cycling into energy, (2) primary consumers (herbivore trophic level) that convert plant energy into animal protein [and energy] and (3) secondary consumers (carnivore trophic level) that prey on primary consumers."

In addition to this static model, ecologists have developed dynamic models about interactions between different trophic levels with a focus on plants and herbivores (McCullough 1997; Schmitz and Saint-Clair 1997) or on the role of predators (e.g., see Hairston et al. 1960; Kirchhoff and Person this volume). Reciprocal herbivore–plant or predator–prey interactions can have effects that alter the abundance, biomass, or productivity of a population, community, or trophic level across more than one link in a food web, in what ecologists have defined as trophic cascades (Pace et al. 1999; Polis et al. 2000). Although such cascades were first described in aquatic ecosystems, leading Strong (1992) to claim that trophic cascades are all "wet," accumulating evidence suggests that they also occur in terrestrial ecosystems (Pace et al. 1999). Many authors still suggest that the effects of trophic cascades on primary producers are weaker in terrestrial than in aquatic food webs (see review of Halaj and Wise 2001). A weaker effect in terrestrial ecosystems was expected to result from the attenuation of effects of herbivores on plants ("top-down" effects) by the antiherbivore defences of plants or from a higher diversity in herbivore species (Schmitz et al. 2000).

The question of trophic cascades has thus been clearly linked to the debate on "top-down" or "bottom-up" control of food web components and thus of species abundance and diversity in a given ecosystem (Pace et al. 1999). The concept of "bottom-up" control assumes that the abundance of primary producers is limited only by the abundance of nutrients, water, and light, the impact of herbivores on plants being controlled by the ability of plants to produce defences. The "top-down" concept stipulates that plants are unable to control herbivores and that the world is green (Polis 1999) only because predators keep herbivores under control.

2. Trophic interactions in the forest of Haida Gwaii: cascade or trickle?

The results of our studies on Haida Gwaii (Queen Charlotte Islands, British Columbia) indicate that the highest abundance and diversity of plants and plant assemblages are observed in the absence of large mammalian herbivores (Stockton this volume). In the presence of a large mammalian herbivore (the introduced Sitka black-tailed deer *Odocoileus hemionus sitkensis*), plant diversity is much reduced, the reduction being strongest on islands with the longest history of deer browsing. Allombert and Martin (this volume) and Martin et al. (this volume) showed that the reduction in plant abundance and diversity is correlated with a reduction in insect abundance and songbird abundance and diversity. Martin et al. (this volume) also showed a web of effects and interactions linking deer, nest predators, and songbird reproductive success. These results suggest that the arrival of the herbivore has initiated a cascade of effects,

flowing from deer down to primary producers and bouncing back to insects and birds.

3. Who is in charge of biodiversity on Haida Gwaii?

In the presence of deer but in the absence of predators, plant and animal diversity are low and are controlled by the abundant herbivore, the effects being only slightly moderated by the presence of plant defences (Vourc'h et al. this volume). This contrasts with what is presumed to have been the original state, before the introduction of deer, in which plant and animal diversity were higher, especially in the shrub layer, and plant diversity was probably controlled by abiotic factors.

When predators affect deer populations, either by causing severe mortality (deer cull experiment, Gaston et al. this volume) or by increasing vigilance costs in response to predation risk (Brown et al. 1999), we observe significant positive responses in plant abundance and diversity (Martin and Baltzinger 2002; Gaston et al. this volume). How comparable species abundance and diversity in forests with deer and predators would be to species abundance and diversity in forests without deer and predators can only be speculated, but our results clearly suggest that in the system studied, the herbivore and its interaction (or lack of interaction) with its predators are key factors controlling biodiversity (see also Kirchhoff and Person this volume).

Given that deer have colonized all but a few small and remote islands, the conclusion follows that on Haida Gwaii, biological diversity in terrestrial ecosystems is largely controlled by deer. This control is most severe in remote protected areas. In areas affected by logging, the impacts of deer and of forestry interact in shaping the living communities.

4. Questions for the Islands

We have shown that the introduction of black-tailed deer to Haida Gwaii has imposed a heavy cost on the biodiversity of the archipelago. While the list of species found in the Islands may have changed little, their relative abundance has changed enormously. Not only do these changes affect the functioning of the local ecosystems, but, by threatening unique island genotypes, they constitute a threat to global biodiversity.

There is much that we would like to know concerning the importance of island populations that research has not yet provided. Haida Gwaii, before the arrival of Europeans, can be seen as a time capsule in which conditions of the early post-Pleistocene were sequestered away from the effects of the ebb and flow of plant and animal populations on the adjacent mainland. Many unique characteristics of the physiology of island populations may have developed, although we have been able to investigate only one example: the chemical defences of the western redcedar *Thuja plicata*. It would be surprising if this were the only such example.

There are many compelling local reasons for trying to reverse the degradation of island biodiversity caused by the deer: matters of ecological, cultural, historical, and recreational significance. However, we should not disregard the importance of Haida Gwaii to the biodiversity of Canada and of North America as a whole. Within the genetic diversity of island populations, genes (alleles) may persist that have disappeared from mainland populations, but which could provide a source of diversity in future. Any erosion of the planet's genetic resources carries potential costs. We need to understand these costs better in order to evaluate the different options open to us in managing the deer.

Currently, the only areas where some kind of control is applied to deer populations are the areas where deer hunting is taking place or, possibly, where black bears are common. An examination of the trends in the number of registered hunters and in the numbers of deer killed suggests that predation by hunting has been decreasing over the past two decades. The recent push to increase black bear hunting may, in its own way, affect predation pressure on deer, which are known as potential prey of bears, at least as fawns.

Another question is this: What consequences will the current reduction in the area of forests cut and the progressive aging of older cuts have on the abundance and distribution of deer in the areas affected by logging? Both trends should lead to less forage for deer. This could result in an increasing pressure on the remaining patches of old-growth forest.

5. Lessons for the mainland

As already suggested by Leopold (1933) and revisited by Stockton (this volume), "when wolves are away the deer will play." The results of the studies conducted by the Research Group on Introduced Species (RGIS) provide strong and convincing arguments to those who in North America or in Europe struggle to convince the public and land managers that without healthy predator populations, currently increasing deer populations will have increasingly negative effects on all components of forest ecosystems. The restoration of predator populations is made even more urgent in the current context of decreasing hunting pressure from humans (or demographically ineffective hunting focusing on antlered deer).

6. Decisions for the future

In the light of the costs imposed on forestry and natural communities by the introduction of deer in Haida Gwaii, it is time to evaluate future options. These fall into two categories: the defeatist (we leave the situation as it is); and the optimist (we attempt to control deer in places and at levels where vegetation recovery is possible).

One of the problems with any action to reduce deer is that, with the population currently controlled by the availability of forage, any population reduction will improve forage and hence will automatically boost deer population growth. The model presented by Kirchhoff and Person (this volume) makes it clear that a recovery of vegetation biomass could trigger an increase in deer population, requiring greater efforts at culling to exert the same control.

Undoubtedly, any action to control deer over the whole archipelago would be extremely expensive. An actual eradication appears so difficult, costly, and contrary to the expressed wishes of the resident community as to be hardly

worth contemplating. If action is to be taken, it seems that it will have to be to reduce deer populations over limited areas. The dissected nature of the archipelago may be helpful in creating areas within which deer reduction could be contemplated. Although deer are capable of crossing substantial water barriers, they almost certainly do so more reluctantly than they would move over similar ground distances. In addition to the two cull islands used by the RGIS, the reduction of deer on other, larger islands could be contemplated: Ramsay and Hibben are obvious examples. However, continued deer culling would be necessary indefinitely. The creation of really large exclosures, perhaps several square kilometres in extent, has the advantage that, following substantial initial expense for fence construction and deer eradication, the ongoing maintenance would be low. Such mega-exclosures could be valuable, especially in areas where great vegetation diversity is anticipated and where fences can be erected away from the possibility of falling trees or branches. For those ecosystems that are found only on Moresby and Graham islands, such large-scale exclosures may be the only feasible method of restoring biodiversity.

Literature cited

Brown, J.S.; Laundré, J.W.; Gurung, M. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. J. Mammal. 80: 385–399.

Hairston, N.G.; Smith, F.E.; Slobodkin, L.B. 1960. Community structure, population control and competition. Am. Nat. 94: 421–425.

Halaj, J.; Wise, D.H. 2001. Terrestrial trophic cascades: how much do they trickle? Am. Nat. 157: 262–281.

Leopold, A. 1933. Game management. Charles Scribner's Sons, New York.

Martin, J.L.; Baltzinger, C. 2002. Interaction among deer browsing, hunting, and tree regeneration. Can. J. For. Res. 32: 1254–1264.

McCullough, D.R. 1997. Irruptive behaviour in ungulates. Pages 69–98 *in* W.J. McShea, H.B. Underwood, and J.H. Rappole (eds.), The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C.

Pace, M.L.; Cole, J.J.; Carpenter, S.R.; Kitchell, J.F. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecol. Evol. 14: 483–488.

Polis, G.A. 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. Oikos 86: 123–155.

Polis, G.A.; Sears, A.L.W.; Huxel, G.R.; Strong, D.F.; Maron, J. 2000. When is a trophic cascade a trophic cascade? Trends in Ecol. Evol. 15: 473–475.

Schmitz, O.J.; Saint-Clair, R.A.E. 1997. Rethinking the role of deer in forest ecosystem dynamics. Pages 201–223 *in* W.J. McShea, H.B. Underwood, and J.H. Rappole (eds.), The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C.

Schmitz, O.J.; Hambäck, P.; Beckerman, A.P. 2000. Trophic cascades in terrestrial ecosystems: a review of the effects of carnivore removals on plants. Am. Nat. 155: 141–153.

Strong, D.F. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. Ecology 73: 747–754.

A conceptual framework for introduced species management in Haida Gwaii

Todd Golumbia and Barb Rowsell

Abstract

Changes created by the arrival of introduced species pose many management challenges (practical, aesthetic, economic, and ecological). If newly arrived species become established and abundant, they will usually have an adverse impact on native ecosystems. While much research focuses on the ecological consequences, both positive and negative aspects from a human perspective are often overlooked. The focus of the Research Group on Introduced Species (RGIS) has, from the outset, been the conduct of research into the ecological relationships among introduced species on Haida Gwaii (Queen Charlotte Islands, British Columbia). In order to develop solutions to the issues identified by research, the findings need to be placed in a human dimensions context. This paper outlines a collaborative process followed in the RGIS research program and the resulting symposium in which local residents and interested groups were brought together with scientists to acquire new information and exchange ideas, thus providing a basis for an introduced species management strategy for Haida Gwaii. The purpose of this paper is to summarize the main perspectives and reflect on the outcomes of the symposium and workshop.

1. Introduction and background

A variety of reasons for species introductions have been summarized in both global and local contexts by Simberloff (this volume), Gaston and Martin (this volume), and Golumbia et al. (this volume). Many introductions have been undertaken with the sole purpose of human benefit, showing little regard for ecological (or other economic) consequences. Changes created by the arrival of introduced species pose many management challenges (practical, aesthetic, economic, and ecological). Some changes can be beneficial to local people in providing new food sources or new opportunities for economic activities. However, if newly arrived species become established and abundant, they will usually have an adverse impact on some native species, with potentially far-reaching ecological effects. Introductions may also affect native organisms of economic or cultural significance. While much research focuses on the ecological consequences, both positive and negative aspects from a human perspective are often overlooked.

The focus of the Research Group on Introduced Species (RGIS) has, from the outset, been the conduct of research into the ecological relationships among introduced species, specifically the Sitka black-tailed deer *Odocoileus hemionus sitkensis*, and the landscape of Haida Gwaii (Queen Charlotte Islands, British Columbia). The principal motivation of researchers was the concern that, aside from the obvious changes to vegetation structure occasioned by the arrival of deer, there might also be cryptic ecosystem effects that might go unnoticed without appropriate research. In order to address these issues with appropriate and effective measures, a deeper and more complete understanding is required. In order to develop solutions to the issues identified by research, we need to place the findings within the existing political (local, provincial, and national governments) and cultural context and to take account of specific interests, such as animal welfare, hunters, and wild-crafters. Gaps between ecological theory and practical conservation (land management, planning, and policy) have resulted in an inability to address critical problems caused by invasive species (Byers et al. 2002). Inadequate information and understanding of the issues can often result in poorly formulated human values, as shown by Porter (1997), and intransigent positions with respect to management of overabundant deer populations.

The best approach to finding solutions is to ensure that all interests have access to all available information before action plans are formulated. Communication can be improved by providing information in formats that are both targeted to specific audiences and accessible to the general public. While provision of information is a focus, there must also be avenues open to receive information from interested and knowledgeable parties. In the end, it is the land managers (often government) who are held responsible for ensuring that they have the best information at hand to find solutions and implement them. These actions are more likely to be successful when a broad consensus has been achieved.

The 2002 RGIS symposium was the culmination of work carried out from 1996 to 2001. The focus of the meeting was twofold: first, to communicate the results of RGIS studies to both peers and local/regional interests; and second, no less important, to put this research in a local context and to provide a venue for discussion to promote community understanding and consensus on issues related to introduced species research and management. In addition

to the work of the RGIS and the experience of other deer researchers dealing with similar and contrasting situations elsewhere in North America, the symposium drew on the perspectives of local people. This was accomplished through structured panel presentations as well as moderated question and answer sessions throughout the symposium. The input from all of these information sources was utilized in the final day for a workshop session to develop goals, objectives, and action items as options for the management of biodiversity in Haida Gwaii.

From the outset, it has been the intent of the RGIS to maximize formal and informal communications to facilitate the exchange of information with the public and with various levels of government (Reeve 1997). This collaborative process was also followed in the symposium, where local residents and interested groups were brought together with researchers at a formal scientific symposium, providing an exchange of ideas among researchers, managers, and the local public. This provides the basis for an introduced species management strategy for Haida Gwaii.

The scientific research findings are presented in this volume by the various authors. However, the flavour of discussion and debate resulting from the public sessions and the workshop has not been captured. The purpose of this paper is to summarize the main perspectives and reflect on the outcomes of the public sessions and the workshop. These results may help promote active management and restoration.

2. A tale of three islands

In an attempt to share our findings "firsthand" with the local communities, a field trip was conducted in 2001 for several community leaders on Haida Gwaii. Preceding the symposium, we repeated this field trip for all of the speakers, a group of land managers, and several local representatives. This group was taken into the field to observe the context for the research and to experience, firsthand, the changes in the forest and shoreline ecosystems of Haida Gwaii. This also provided an opportunity for relaxed discussion among the various parties. The groups were transported by floatplane and motor vessel to three islands in Laskeek Bay that formed part of the "natural laboratory" of the RGIS. These islands demonstrate ecosystems that are heavily deer-impacted, deer-free, or recovering from deer impact.

The visit started at East Limestone Island (48 ha), which contains forests that have been heavily browsed by deer. Typical vegetation appears like an open park-like landscape with a mossy understory, the virtual absence of a shrub layer, a total absence of regenerating western red cedar *Thuja plicata*, and delayed regeneration of Sitka spruce *Picea sitchensis*.

The groups next visited Low Island (10 ha), where remoteness, relatively small size, and rugged coastline have combined to prevent colonization by deer. On Low Island, a profusion of flowers grows in every crack and soil patch along the rocky shoreline. This contrasts strongly with the barren shores of East Limestone Island. The forest interior is equally remarkable, with dense shrubs and ferns challenging navigation. The plant communities vary from coastal salmonberry *Rubus spectabilis* groves, penetrated only on hands and knees, to an open mix of salal *Gaultheria shallon*, red huckleberry *Vaccinium parvifolium*, and ferns in the forest interior.

Finally, the group embarked for Reef Island (249 ha), where, until 1997, about 80 black-tailed deer were known to reside, resulting in conditions similar to those on East Limestone Island. Between 1997 and 2000, deer were culled, and the recovery has been closely monitored. Stunted spruce now exhibit vigorous growth; veteran 70-year-old red huckleberry stems are producing new shoots that now reach heights of 1.5 m; and slopes are covered with ferns or shrubs. Prior to the cull, not a single cedar seedling was observed in the vegetation samples: now, they are a common sight. The pattern on the shoreline is similar, confirming that when browsing pressure is sufficiently reduced, plants that seemed to be entirely extirpated can recover in a short period of time (Gaston et al. this volume).

3. Deer introduction and management: Panel members' perspectives

Directly following the field trip, a public panel discussion was held in the village of Skidegate to provide an opportunity for local people to "kick off" the symposium with local perspectives on introduced deer. A moderated discussion followed. The panel participants presented their perspectives in the opening session and, after participating in the 2 days of symposium proceedings, were invited back to address the workshop and provide their key objectives with respect to deer management and, more generally, for all introduced species on Haida Gwaii. In addition, objectives were also presented for the RGIS, the Council of the Haida Nation, and provincial and federal government agencies.

3.1 Barb Wilson (a Haida perspective)

Since the introduction of deer, berry pickers have gone from being carefree, shaking untold amounts of berries from the bushes into our aprons, to picking them one by one and carefully putting them in a bucket. This was my realization after a recent berry-picking expedition with my colleague Anna Gajda. In further talks with Haida people and my own observations in field research, I realized that this reflects the state of many traditional plants that our people use for food, medicine, and fibre. The Haida have a long tradition of gathering plants. Our lives and customs have evolved as the land has evolved. We are here to be caretakers to all that is here with us. How did we miss what is happening to our plants? Our plants are disappearing! In the space of 125 short years, almost all of our berries, not to mention medicinal, food, and fibre plants, have become scarce, if not threatened. Not all Haida have lost the thread of how to use and look after the plants. We must also look to education and learning of the traditional ways to protect the plants. Deer are an important source of protein for many families here on Haida Gwaii, but not as necessary as when they were first introduced in the early 1900s.

3.2 John Cumming (a hunter's perspective)

Deer were introduced to Haida Gwaii as a food source, and this goal has been achieved. As far as deer

management goes, I was inclined to say, "that is a problem for the logging industry." Perhaps it is just the cost of doing business here. We must define what it means to "control" deer. If it means eradication, I don't agree. Any large-scale attempt to remove deer from the Islands would be expensive and unsuccessful. The introduction of predators would not be an effective management strategy either. Eventually a balance will be struck between deer populations and habitat.

I hunt because I don't like the taste or the questionable quality of commercial beef. I enjoy the search for my prey and the pleasure of being outdoors. I do not have any moral qualms about killing animals for food. The best management option to curb deer populations is improved effectiveness of human hunters—likely the only acceptable means of deer control. Changes to hunting regulations to allow higher bag limits and an extended hunting season would increase the numbers of deer killed each year. I would like to see those who hunt able to supply those who cannot. Also, road deactivation should be done in a manner that still allows access to good hunting areas.

I have no issue with the RGIS and their research on the impact of introduced species. I do think, however, that communications should be improved, specifically with the Island communities. I think that RGIS results should be put in lay terms so that the people of Haida Gwaii can get a better understanding of the science behind the issues. I would like to see a more broad-based approach to the impacts of all introduced species. I would also like to see more participation by Island residents, and I want hunting to continue to be a part of life here.

I have to thank the group for giving me a broader view of the effects of deer, for I have found that I had a rather narrow view on this subject prior to the conference. It was very interesting to realize that what is happening here on the Queen Charlotte Islands is by no means unique; deer are taking over in other places. I also find it interesting that hunting was successfully used as a population management tool. I had not given much thought to the effect that deer have on the life systems here. It surprised me that deer browse affects the insects and songbirds to the degree that it does. Information on the importance of many plants to the Haida culture made me far more sympathetic to arguments in favour of deer control. The arguments put forward by the forest industry have always seemed purely based on financial benefit; I find it hard to get too upset about profit loss. I would like to think further about all the information I have been given, but maybe I can accept the need to limit and control the deer population on the Islands.

3.3 John Barker (a forester's perspective)

Foresters have long recognized that deer represent a problem, not only to the ecology of the Islands, but also to many aspects of forest management. Some of these influences are increased constraints on the land base, limited species choices, delayed regeneration, slow early growth, increased regeneration costs, increased erosion damage, depleted habitats, and reduced biodiversity. The problem has long been known, although the cost pressures have more recently intensified. For example, on better cedar sites, cedar can be regenerated. We know what the problem is, and we have identified what is possible with respect to seedling protection, and we also recognize the significant cost of protection, which is hard to justify in today's economy.

What has not been explored or implemented in any meaningful way is deer management. There is sufficient knowledge now to begin deer control measures. If we are to effectively manage the ecosystems of the Islands, we need to act now. There are a number of things that can be done, but some approaches may be politically or legislatively difficult to deal with. Three options present themselves:

1. Deer farming provides a profit potential through marketing of meat and other products. The incentive to develop business has proven successful in New Zealand.
2. Deer eradication was tried in New Zealand for over 100 years without success and would not likely be successful here.
3. Introduction of predators would likely be successful. However, there are ecological and social uncertainties associated with yet another introduction.

Although I have been coming to Haida Gwaii and working in the forest here for 40 years, the issue of introduced species is something that should be decided by the residents of the Islands. You must have a vision of what you would like to accomplish and make a plan for the selected level of management. There is a problem of scale in planning and what is possible to accomplish. Coordination of efforts is the key to success. For the effort to be successful, Islanders need to "buy in" to the project and be involved. To get this support, it will be necessary to communicate the message to residents and politicians. Hunting regulations may have to be changed to be flexible and locally applicable. It is also important to work with foresters to develop silviculture practices that will assist in a deer management plan. It has taken many years for the problems of introduced species to develop, and it will take many years to find and implement solutions.

3.4 Terry Husband (a resident's perspective)

My family has been here for a long time, and I have lived here all of my life. I started to hunt and fish as a child with my father, uncles, and grandmother. I have worked in logging and fishing and look at all of it as a great opportunity to learn about my environment. My father remembers when deer first became abundant after introduction. The big fire in the 1800s that burned the Tlell and Yakoun watersheds provided good habitat for the deer to flourish. Since the forest has regrown in these areas, the elk have become more plentiful than deer.

In high numbers, deer can be a safety issue. Anyone who has lived on these Islands for any length of time will have had an encounter with deer on the roads. I have learned that there are other values to be considered when thinking of deer—for instance, the impact of deer browse on berries that many people like to collect and cedar trees that are important in forestry as well as monumental artworks. Deer are opportunistic animals and take advantage of openings

in the forest, both natural and man-made, and these become high-impact areas.

I have participated in the RGIS deer culls, and, for me, this was an education in deer behaviour and hunting. I found it very interesting to work with scientists for the purpose of research and restoring the habitat of these representative islands. These are small but rugged islands, and we found that deer can travel far more easily than hunters. Deer culls are important; they provide relief for the vegetation and a chance to see what the ecosystem would be like without deer browse, but the time, money, logistics, teamwork, and effort involved would physically prohibit removing the deer from all of Haida Gwaii by this method.

Deer are important to these Islands; they are a valuable asset for food and recreation, and we can't just treat them as pests. It is important to look at the overall picture. We need cooperation and concessions among all people and organizations on Haida Gwaii if we are going to be able to find solutions. I hope that the scientists will stay and continue to help us find these solutions.

From the conference, I got a sense of urgency, that we are on the edge of having a vision to begin working on introduced species management. I agree with other speakers about changes to hunting regulations, implementing changes to road deactivation, building exclosures, and restoring small islands. We have got a lot of information, and the time to act is now.

3.5 Council of the Haida Nation Forest Guardians—Gwaai Edenshaw, with excerpts from Engelstoft and Bland (2002)

The Forest Guardians have five objectives that we would like to see come out of this initiative: 1) recognition that culture is a relationship to the land; 2) maintain or return biodiversity on the Islands; 3) hold forestry licensees to logging practices that are responsible and sustainable; 4) create a 1000-year plan for cedar so that cedar of all ages can grow and thrive to provide material for our future generations; and 5) work with all agencies, organizations, and people of like mind to achieve these goals.

Life on Haida Gwaii has evolved as a delicate balance over thousands of years in isolation from the mainland. Haida culture has developed with respect to this balance that provides for health and well-being. Haida Gwaii is one ecosystem; if any part of it is ruined, it affects other parts, including the health of the people and culture. As a government, the Council of the Haida Nation is responsible for ensuring that all people respect Haida relationships to the land and for developing initiatives that are based on a holistic view of the island ecosystem.

Although industrial resource extraction has been the primary threat to the diversity of life on the Islands, the added stress of nonnative species has become increasingly apparent to our people. Several organizations have developed projects to raise awareness and understanding of how some introduced species are affecting the ecology of Haida Gwaii.

A strategic approach to restoration of terrestrial ecosystems has been identified as a major priority within the land use plan currently being developed by the Council of the Haida Nation. In April 2001, the Council signed a protocol with the B.C. government to move forward with a land use planning process based on ecosystem-based forestry principles in cooperation with local communities and all levels of government. Land use planning will develop a protected areas network, identifying areas for ecosystem-based forestry and opportunities for restoration.

3.6 Research Group on Introduced Species—Jean-Louis Martin

The focus of the RGIS has been to understand the ecological functions of introduced species and the changes brought about by them. The RGIS has tried, whenever possible, to share the results with end users and the local community. These research activities should be integrated with an overall vision for introduced species management on Haida Gwaii, including, for example, expansion of research to other invasive species or proactive management actions such as restrictions on the importation of additional exotic species. The RGIS work has resulted in the acquisition of a significant capital of knowledge that is available for future use. There is also the capital of ongoing experiments with a potential to contribute even more to the knowledge. A remarkable field laboratory is another valuable asset that could be viewed as a benefit for the entire island community.

The RGIS considers any attempt to eradicate deer on Haida Gwaii as extremely difficult and, given the value of deer, not socially desirable. In contrast, we think that deer should be managed in a way that reduces deer browsing impacts and enhances biodiversity. The RGIS agrees with other workshop participants that a consultative group or committee made up of land managers, science/research expertise, and stakeholders is required to advise on conservation/biodiversity issues related to introduced species. Based on the knowledge gained to date, the highest RGIS concerns and priorities are to 1) maintain low deer populations on the cull islands so that we can continue to learn from them; 2) broaden research to additional relevant deer research objectives (e.g., demography and population health, bear impact on deer, deer impact on alpine/subalpine vegetation, between-island deer movement); and 3) develop additional relevant research objectives to address knowledge gaps relative to other introduced species (e.g., invasive plants, raccoon *Procyon lotor*, American red squirrel *Tamiasciurus hudsonicus*, and beaver *Castor canadensis*).

3.7 B.C. Ministry of Water, Land and Air Protection—Tom Smith

Historically, there has been a laissez-faire attitude towards introduced deer management on Haida Gwaii. The unique situation of deer abundance and lack of predators has led to a history of liberal hunting regulations, although these regulations were never designed as a vegetation management tool. The deer management objectives from the Ministry would be to 1) have everyone reach consensus on proposed changes to hunting regulations; 2) maintain hunting opportunities and access to hunting areas; 3) reduce the current deer population—neither the deer nor their habitat is currently healthy; and 4) increase education programs for the public and also for politicians and civil servants whose

concept of deer management may be limited to preserving or enhancing deer populations rather than achieving larger objectives, such as vegetation and habitat management.

Required changes in legislation may not be easy. These changes will set precedents, about which governments are cautious. When considering legislation changes to use hunting as a management tool, the Ministry must also look at the policy of deer tags as a revenue producer, must consider the humane aspects related to deer reduction, and must consult with First Nations on any changes. With respect to predator introduction, the Ministry would be very cautious. The predators are themselves introduced species, and we are not able to fully predict the outcomes of such introductions.

3.8 Parks Canada—Dennis Madsen

Gwaii Haanas National Park Reserve and Haida Heritage Site is bound by the *Canada National Parks Act* and must be managed accordingly. The legislated priority is "maintenance or restoration of ecological integrity through the protection of natural resources and natural processes." It is our policy to base decision-making on scientific information, such as that provided by this conference. Our policies are generally in line with the objectives of the other speakers. Gwaii Haanas sees the protection and conservation of representative ecosystems as our key objective. To do so, it will be important to 1) continue addressing information gaps; 2) monitor the long-term trends of deer affected and restored areas; 3) continue to work in cooperation with others on Haida Gwaii to manage the effects of deer; and 4) continue efforts on outreach and communication.

4. Lessons learned: Summary of RGIS workshop outcomes

The workshop began with an overview of key research findings and key objectives described by participants (see above). The remainder of the day was dedicated to working in small groups to synthesize a set of common goals, objectives, and action items charting a course for the future—essentially, the construction of a management framework for introduced species. The outcome of this workshop will provide direction to land managers for implementation of any follow-up initiatives.

While many goals were discussed, the workshop participants distilled the discussion down to four "main" goals. These were:

1. Maintain and restore native biodiversity, species at risk, and culturally significant plants and animals (including deer) in our island ecosystems.
2. Reduce the impacts of deer on our native ecosystems.
3. Establish a locally based working forum to consider, recommend, and communicate issues related to all introduced species and to provide a clear vision with consensus.
4. Communicate, educate, and continue dialogue on issues of biodiversity and the impacts of introduced species.

Three objectives were identified to address these goals. A number of "action items" were presented for each objective during a brainstorming session. These were distilled to a small number of priority items:

1. Communicate and educate
   - Utilize a locally based forum to manage and disseminate information, report on progress, and develop consensus.
   - Disseminate current and consistent messages on various aspects of biodiversity and introduced species, as well as human interest groups and management jurisdictions.
   - Find new means to reach people, including more interaction with local schools.
   - Expand media outreach to include general awareness and prevention of new introductions.
   - Continue field tours with partners to provide firsthand experience with the issues.
2. Active management
   - Maintain existing culls.
   - Undertake a cost–benefit feasibility analysis for deer management options, including, but not limited to, communal or commercial hunting, immunocontraception, and trained dogs.
   - Engage the land use planning forum to establish management zones with different biodiversity emphasis in relation to deer.
   - Investigate changes to road deactivation and access.
   - Modify existing hunting regulations (bag limits, extended doe season, earn-a-buck program).
   - Develop a process for access points (ferry landings and airports) to limit new introductions.
   - Encourage invasive plant removal and proper destruction.
   - Discuss the implementation of a bounty on introduced fur bearers (raccoon, beaver, and red squirrel) with local trappers.
   - Continue to eradicate raccoons on seabird colonies; expand culling to neighbouring areas.
   - Focus hunting and trapping effort by using facilitated access in targeted areas.
3. Research and monitoring
   - Maintain monitoring of cull islands and related exclosures.
   - Measure the effect of deer on alpine/subalpine vegetation.
   - Pursue good ecological mapping for habitat modelling.
   - Undertake predator (black bear *Ursus americanus*) research (diet study, density, and population).
   - Integrate Alaskan deer model to form model for black bear predation.

- Carry out fundamental deer research to understand spatial variation in deer densities, deer reproductive rate, and deer movement to determine deer density thresholds in relation to recovery of vegetation.
- Utilize hunters to establish a long-term monitoring program for deer (pregnancy rate, morphology).
- Identify knowledge gaps in research, and start research on other introduced species.
- Continue with the geographic information system tracking database for all invasive species.
- Collect data on Aboriginal deer hunting.
- Study the relationship between forest management and deer density, with a focus on using silvicultural tools to mitigate deer browsing impacts.

5. Discussion

Without an open exchange of information and ideas between all interested or affected parties, meaningful strategies for dealing with deer in Haida Gwaii will not be achieved. The work of the RGIS was greatly enhanced by the inclusion of local people in the design and implementation of the research program. The Laskeek Bay Conservation Society, a broad-based local conservation organization dedicated to environmental education through monitoring and research, was a partner in the project from its inception and provided continuous feedback on local perspectives, as well as providing information on the local skills and knowledge available in this remote archipelago. Engaging local support at the outset enhanced the research program and also offered a conduit for outreach to the local communities. This relationship also maximized the fusion of local know-how and understanding with "imported" science expertise. There was, and continues to be, a constant interaction informing the local people about introduced species and biodiversity and educating the scientists about the context of their work on Haida Gwaii.

It is promising to see other initiatives now being undertaken that will complement the work of the RGIS. Under the auspices of the Terrestrial Ecosystem Restoration Program, the Council of the Haida Nation and the B.C. Ministry of Water, Land and Air Protection undertook a program to survey local residents and resource managers with expertise in introduced species to develop a strategic plan for the assessment of threats from introduced species and implementation of restoration activities to address these threats (Engelstoft and Bland 2002). To succeed, however, these strategies need a sound base of information on the spread, ecological effects, and control of introduced species (Byers et al. 2002). It is also promising to observe, both prior to and immediately following the RGIS symposium, several initiatives to take action on mitigation of introduced species threats, ranging from self-directed removal of Scotch broom *Cytisus scoparius* by Tlell residents to the designation and protection of culturally significant plant communities directed by Daamaan Xil—a group of Haida elders "taking care of the plants" and the Council of the Haida Nation Forest Guardians. More proactive measures, such as exclusion of further introductions, may be most effective from a conservation concern, but are likely to be most difficult in implementation. Invasion pathways and the frequency of species introduction are dependent on patterns of trade and travel. This is exacerbated by the current trends to liberalize regulatory regimes and the fact that containment or prevention measures will only be as good as the measures taken by the least effective party (Perrings et al. 2002). Although intended in a global and international context, this issue will also have consequences locally, as there is often more than one clear line of authority on these issues and limited capacity, or often interest, to deal with issues of quarantine or control.

By applying a continuous effort and ensuring continued flow of information in both directions, all parties were empowered. The RGIS has always recognized that its role is to provide unbiased and objective information to facilitate important decision-making at the local and regional political levels. As we move from discussion into action, strong relationships have been forged, and the transition from information gathering to management decision-making should be easier. The outcome of the RGIS symposium and workshop seemed to fall into place with little effort. In the few months following the workshop, a group of local residents with an interest in pursuing these initiatives was formed. The introduced species task force has initiated several action items and is actively supporting similar initiatives from local people. Simultaneous to this and as a direct outcome of the symposium, provincial wildlife managers are actively pursuing changes to the hunting regulations for Haida Gwaii deer and, in so doing, are changing the focus from traditional wildlife management to a more vegetation-sensitive ecosystem management approach. Introduced species have been placed at the forefront for both land use planning and species at risk recovery strategies for the archipelago.

Unanswered questions remain, and, prior to scaling up restoration initiatives, questions related to patterns of spread and abundance, system invasibility, and impact thresholds will have to be addressed. These answers will have to be phrased in terms of risk assessment and feasibility. In order to measure our effectiveness in these ventures, it will be essential to have defensible monitoring protocols. There is, most often, little information on the effects of introduced species, but there is even less information on the effects of control efforts on the communities and species we are attempting to restore (Byers et al. 2002). The task force sees these areas of study as a future role for the RGIS or what may follow from the RGIS. Input and guidance from local advisory bodies have proven useful in other deer management scenarios (Shafer-Nolan 1997) and can likely be applied to other introduced species on Haida Gwaii as well. By combining objective science with local context, basing management decisions on that sound science, and openly discussing available options for resolution (open decision-making process), it is possible to generate broad public support for addressing potential controversial issues (Mitchell et al. 1997). The continued cross-fertilization of local knowledge and either local or "imported" scientific expertise will provide the best approach for capacity building

and success in the future. Similarly, the mix of hands-on action, administrative adjustments, education, and objective scientific research and monitoring will ensure that the best approaches are being considered, implemented, and followed up.

Acknowledgements

We thank the panel members and approximately 50 workshop participants who have contributed their ideas and energy towards discussions and actions on the management of introduced species on Haida Gwaii. Much of the information for this paper was gleaned from interviews and discussions leading up to and following the symposium and through the panel and workshop sessions during the workshop.

Literature cited

Byers, J.E.; Reichard, S.; Randall, J.M.; Parker, I.M.; Smith, C.; Lonsdale, W.M.; Atkinson, I.A.E.; Seastedt, T.R.; Williamson, M.; Chornesky, E.; Hayes, D. 2002. Directing research to reduce the impacts of non-indigenous species. Conserv. Biol. 16(3): 630–640.

Engelstoft, C.; Bland, L. 2002. Restoration priorities associated with introduced species impacts on Haida Gwaii/Queen Charlotte Islands: Perspectives and strategies. Unpublished report, Council of the Haida Nation Forest Guardians and B.C. Ministry of Water, Land and Air Protection, Victoria, B.C. 112 pp.

Mitchell, J.M.; Pagac, G.J.; Parker, G.R. 1997. Informed consent: Gaining support for removal of overabundant white-tailed deer on an Indiana state park. Wildl. Soc. Bull. 25(2): 447–450.

Perrings, C.; Williamson, M.; Barbier, E.B.; Delfino, D.; Dalmazzone, S.; Shogren, J.; Simmons, P.; Watkinson, A. 2002. Biological invasion risks and the public good: an economic perspective. Conserv. Ecol. 6(1): 1. Available at http://www.consecol.org/vol6/iss1/art1.

Porter, W.F. 1997. Ignorance, arrogance and the process of managing overabundant deer. Wildl. Soc. Bull. 25(2): 408–412.

Reeve, M. 1997. Introduced species communications strategy—draft. Unpublished report produced by Parks Canada Agency for the Research Group on Introduced Species. 9 pp.

Shafer-Nolan, A.L. 1997. The science and politics of deer overabundance at Cyahoga Valley National Recreation Area, Ohio. Wildl. Soc. Bull. 25(2): 457–461.