Birds in boreal Canada

by Anthony J. Erskine

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The author

Anthony J. (Tony) Erskine has been employed by the Canadian Wildlife Service (CWS) in various capacities since 1960. Born in England, he came to Canada in 1936. His university career included the degrees of B.Sc. from Acadia University, and M.A. and Ph.D. from Queen's University, all in chemistry, and subsequently M.A. in zoology from the University of British Columbia. After joining CWS he worked on waterfowl, particularly the life history of the Bufflehead and population studies on mergansers. While carrying out the work described in this report, he was research scientist in the Populations and Surveys Division, Migratory Birds Branch, CWS, in Ottawa, with responsibilities covering non-game birds across Canada. He has recently been appointed Chief, Migratory Birds Division, Atlantic Region, CWS, with headquarters in Sackville, New Brunswick.

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This study makes use of data collected over a 30-year period by many different people, and it is not possible to name individually all those whose efforts contributed to it in some way. Many are cited in the reference list and not mentioned further here.

My field work was assisted by many people. In particular, P. A. Pearce, S. Lunn, and S. Robinson helped with selecting and setting up plots in 1968, D. Forsyth and N. Garrity in 1969, R. Watt in 1970, W. Scott in 1971, P. Sweatman in 1972, C. Cuthbert in 1973 and 1974, and M. Perry in 1975. Watt and Cuthbert also contributed bird observations during the setting-up periods in those years. R. H. Lamont and A. Kabzems suggested suitable locations for study areas in balsam fir in Manitoba and Saskatchewan respectively.

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Abstract

Birds of the boreal regions of Canada were studied over an eight-year period to assemble baseline data on the composition and density of the bird communities in various habitat types. These data, with other material from a variety of sources, now permit an overall review of the boreal avifauna, its composition, evolution, and prospects for survival.

All boreal conifer forests share the same community of birds, with some additions or subtractions, whereas much greater differences are found in comparison with conifer habitats of other, nearby regions to the south, where such communities do not form the vegetational climax. The regular and abundant members of the conifer forest avifauna include Spruce or Ruffed Grouse (Tetraonidae), Canada* or Blue Jays (Corvidae), Boreal Chickadee (Paridae), Swainson's Thrush (Turdidae), Golden- and Ruby-crowned Kinglets (Sylviidae), Magnolia and Yellow-rumped Warblers (Parulidae), Northern Junco*, and Chipping or White-throated Sparrows (Fringillidae), plus the cardueline finches. Densities of breeding birds rise through the succession, from 100 to 200 pairs per km² in open jack pine stands or low bog forests through 200 to 400 pairs per km² in spruce to 300 to 600 pairs per km² in balsam fir, the richest conifer habitat in the boreal region. Still higher densities, up to over 800 pairs per km², occur in the presence of spruce budworm outbreaks, owing to the response of a few warbler species to this food source, and in mixed coniferous-deciduous stands.

Broad-leafed forests in the boreal region are relatively limited both in duration on a site and in site variety, and they lack a unique bird community. Birds of such sites are drawn partly from the eastern deciduous fauna and partly from that of successional conifer habitats. The regular and abundant members of this group include Ruffed Grouse (Tetraonidae), Yellow-bellied Sapsucker (Picidae), Least Flycatcher (Tyrannidae), Black-capped Chickadee (Paridae), American Robin and either Swainson's Thrush or Veery (Turdidae), Red-eyed Vireo (Vireonidae), Chestnut-sided and Mourning Warblers, Ovenbird, and American Redstart (Parulidae), and Rose-breasted Grosbeak (Fringillidae). West of the Rocky Mountains, Dusky Flycatcher and Western Wood Pewee (Tyrannidae), Warbling Vireo (Vireonidae), Orange-crowned and MacGillivray's Warblers (Parulidae) at least partially replace other members of the same families. Densities of breeding birds fall to the north and west, from between 400 and 600 pairs per km² in New Brunswick to Ontario, down to 200 to 300 pairs per km² in northern British Columbia, but rise again west of the Rockies.

All birds of open habitats in the boreal region also occur in other biomes, for example: Sharp-tailed Grouse (Tetraonidae), Killdeer (Charadriidae), Common Nighthawk (Caprimulgidae), and Savannah Sparrow (Fringillidae). Many widespread species also occur in the low shrubby stages of early forest succession, including Alder Flycatcher (Tyrannidae), House Wren (Troglodytidae), Robin and Hermit Thrush (Turdidae), Mourning Warbler and Common Yellowthroat (Parulidae), American Goldfinch, Northern Junco, White-throated and Song Sparrows (Fringillidae). Many others are associated with edges, both those between forests and open areas within the region, and with adjoining open biomes. Bird densities in open habitats are typically lower than in forest, usually in the range from 150 to 450 pairs per km².

Wetland birds are less evenly distributed than those in terrestrial communities, and quantitative data are less satisfactory. Recognizable groupings include birds of deep marsh, of open water, and of shallow marshes, fens, and assorted bogs, the last probably the wetland types most typical of the boreal region. Most birds are restricted to one or a few of these wetland groups, but the interdigitation of the types means that many wetland birds are widespread and abundant, for example: Mallard, Green-winged Teal, Lesser Scaup (Anatidae), Common Snipe (Scolopacidae), Alder Flycatcher (Tyrannidae), Yellow Warbler, Northern Waterthrush, and Common Yellowthroat (Parulidae), Red-winged and Rusty Blackbirds (Icteridae), Savannah, Lincoln's, Swamp, and Song Sparrows (Fringillidae). Density data are lacking except for some types of bogs, in which densities seldom exceed 100 pairs per km²; more fertile types of wetlands probably support much higher densities of birds.

Artificial environments include those cleared for agriculture or right-of-way, and artificial structures such as buildings and dams. Birds of the open habitats are associated largely with remnants of shrubbery, or with the edges between disturbed and more natural areas, but a few such as Killdeer (Charadriidae) and Savannah Sparrow (Fringillidae) are almost ubiquitous. Urban settlements feature especially three introduced species, plus four swallows (Hirundinidae), American Robin (Turdidae), Chipping and Song Sparrows (Fringillidae). Densities in towns vary directly with time

* Note on bird names: English names follow those of the AOU Check-list (1957) and its Supplements (1973, 1976), except for Canada Jay (in preference to Gray Jay), and Northern Junco (in preference to Dark-eyed Junco as in ABA Checklist, [1975]). Separate names for those forms reduced to subspecific rank in the AOU Supplement (1973) have been used where appropriate.

since development and inversely with latitude, ranging from 200 to 600 pairs per km²; generally such densities are as high as those in nearby natural habitats, but with fewer species than in woodland.

The boreal avifauna of Canada includes species with their centres of abundance within this region, and also elements from adjoining regions, particularly the deciduous and transition forest regions to the southeast. Distribution patterns of closely related species pairs and of subspecies within a species indicate the main faunal breaks within the boreal avifauna to be along the line of the Canadian Rockies and between Lake Superior and Hudson Bay; other important breaks along the British Columbia Coast Range and across south-central British Columbia form the southwestern borders of the boreal region as here understood. Few species are confined to boreal conifer forests, and these mostly are of holarctic families, genera, or species. The rest are either of other habitats, or else tolerant of a variety of forest types, particularly the broad-leafed forests of eastern North America in which many families originated.

More than 80% of all bird species breeding in or to the north of the boreal region winter farther to the south. Of the migrant land birds, roughly half the species winter south of 30°N, in tropical or subtropical regions. We do not know whether the distribution of individuals parallels that of species. Most species that winter in the boreal region are year-round residents of the boreal forest, and the rest are birds of the subarctic ecotone which winter in open areas within, as well as to north and south of, the boreal region. Most migrant species spend only from three months (obligate insect eaters) to five months (insectivores which also eat seeds and fruit) in the boreal region, and thus largely depend on more southern biomes for their continued survival. Most of the residents exhibit irruptive behaviour, sometimes accompanied by opportunistic breeding. Collectively, boreal birds seem an adaptable group, able to cope with the gradual shifts of their habitats over glacial epochs, as well as with sweeping seasonal movements between biomes in the course of annual migrations.

The impact of man on boreal birds has been less than in most biomes long settled by man; this tends to support the popular misconception that the resources of this region are inexhaustible. Extraction of mineral resources has created deserts locally, but as yet nowhere on a scale such as to threaten bird species' existence. Agriculture has also been of minor significance. Trends toward shorter turnover cycles in forestry could threaten mature and particularly old-growth forests, but transportation costs are likely to limit such effects to the more accessible regions. The birds characteristic of the most fertile, climax forest stands seem tied to the richest types available in an area, rather than to any particular forest type throughout their range, but all the richer forests are likely to be early targets for exploitation when this occurs. Hydro-electric developments destroy the often fertile riparian communities, though here, too, most of the species involved are widespread and/or tolerant of a variety of habitats. Toxic chemicals threaten a number of raptorial or fish-eating birds which receive high concentrations of these poisons through extended food chains. Canadian ecosystems are not isolated, but are parts of hemispheric migration systems for birds and of a global system subject to man's exploitation.

Résumé

Les oiseaux des régions boréales du Canada ont été étudiés huit ans durant afin de réunir des données fondamentales sur la composition et la densité des milieux d'oiseaux de divers biotopes. Ces données, ainsi que d'autres renseignements de diverses sources, permettent d'avoir maintenant une vue d'ensemble de la composition, de l'évolution et des chances de survie de l'avifaune boréale.

Les forêts boréales de conifères partagent à peu près toutes la même gamme d'oiseaux; plus au sud, par contre, où les peuplements de conifères n'arrivent pas au climax, la gamme des oiseaux varie bien plus d'une forêt de conifères à l'autre. L'avifaune de la forêt de conifères comprend habituellement de nombreuses populations de Tétras des Savanes et de Gelinotte huppée (*Tétraonidae*), de Geai du Canada* et de Geai bleu (*Corvidae*), de Mésange à tête brune (*Paridae*), de Grive à dos olive (*Turdidae*), de Roitelet à couronne dorée et de Roitelet à couronne rubis (*Sylviidae*), de Fauvette à tête cendrée et de Fauvette à croupion jaune (*Parulidae*), de Junco ardoisé*, de Pinson familier et de Pinson à gorge blanche (*Fringillidae*), ainsi que de chardonnerets du genre Carduelis. Plus la forêt est à un stade avancé de la transition, plus forte est la densité de ses populations d'oiseaux nicheurs: de 100 à 200 couples au km² dans les peuplements clairsemés de pin gris ou dans les tourbières, de 200 à 400 couples dans les peuplements d'épinettes et de 300 à 600 dans les peuplements de sapins baumiers, le plus riche biotope à conifères de la forêt boréale. La densité s'accroît davantage encore, jusqu'à 800 couples au km², là où pullule la tordeuse des bourgeons de l'épinette, dont se régalent certaines espèces de fauvettes, ainsi que dans les peuplements mixtes de conifères et de feuillus.

Les forêts de feuillus ne présentent en régions boréales que peuplements chacun d'assez faible hététogénéité, à station plutôt brève. Elles n'abritent pas de gamme d'oiseaux qui leur soit propre. On y trouve un apport et de l'avifaune des forêts à feuillus de l'est et de celle des forêts de transition à conifères. Les espèces géné-

* Les noms anglais des oiseaux sont conformes à la nomenclature de l'American Ornithological Union Check-list ainsi que de ses suppléments de 1973 et de 1976 sauf pour ce qui est du Geai du Canada (Canada Jay) et du Junco ardoisé (Northern Junco), appellations qu'on a respectivement préférées à celles de Geai gris (Gray Jay) et de Junco à dos roux (Dark-eyed Junco, comme dans l'A.B.A. Checklist, 1975). On a utilisé le cas échéant des noms distincts pour les formes que le supplément de 1973 de la nomenclature de l'A.O.U. a réduites au rang de sous-espèces.

ralement bien représentées en pareil cas comprennent la Gelinotte huppée (*Tétraonidae*), le Pic maculé (*Picidae*), le Moucherolle tchébec (*Tyrannidae*), la Mésange à tête noire (*Paridae*), le Merle d'Amérique et la Grive à dos olive ou la Grive fauve (*Turdidae*), le Viréo aux yeux rouges (*Viréonidae*), la Fauvette à flancs marrons, la Fauvette triste, la Fauvette flamboyante (*Parulidae*), ainsi que le Gros-bec à poitrine rose (*Fringillidae*). À l'ouest des Rocheuses, le Moucherolle sombre et le Pioui de l'Ouest (*Tyrannidae*), le Viréo mélodieux (*Viréonidae*), la Fauvette verdâtre et la Fauvette des buissons (*Parulidae*) remplacent au moins en partie les espèces des familles correspondantes. La densité des populations d'oiseaux nicheurs décroît à mesure qu'on va vers le nord et vers l'ouest, de 400 à 600 couples le km² au Nouveau-Brunswick et en Ontario, à 200 à 300 couples du km² dans le nord de la Colombie-Britannique. Toutefois, elle augmente de nouveau à l'ouest des Rocheuses.

Tous les oiseaux des biotopes à découvert de la région boréale se rencontrent aussi en d'autres aires biogéographiques. Ainsi en est-il de la Gelinotte à queue fine (*Tétraonidae*), du Pluvier kildir (*Charadriidae*), de l'Engoulevent commun (*Caprimulgidae*) et du Pinson des prés (*Fringillidae*). Bien des espèces fort répandues se rencontrent aussi dans l'étage arbustif des jeunes forêts à l'amorce de la transition: le Moucherolle des aulnes (*Tyrannidae*), le Troglodyte familier (*Troglodytidae*), le Merle d'Amérique et la Grive solitaire (*Turdidae*), la Fauvette triste et la Fauvette masquée (*Parulidae*), le Chardonneret jaune, le Junco ardoisé*, le Pinson à gorge blanche et le Pinson chanteur (*Fringillidae*). Bien d'autres espèces fréquentent les lisières, tant des forêts et des terrains découverts au sein d'une même région que celles qui font transition d'une aire à l'autre. Il est typique des biotopes découverts que la densité des populations d'oiseaux y soit plus faible, y variant habituellement de 150 à 450 couples au km².

La répartition des espèces qui hantent les mouillères est moins uniforme que celle des populations terrestres et les données quantitatives au sujet de celles-là laissent davantage à désirer. On y peut discerner les oiseaux de telles catégories que ceux des marais profonds, ceux des aires complètement submergées, ceux des marécages peu profonds et ceux des tourbières qui, de toutes les mouillères, constituent probablement le biotope le plus typique de la zone boréale. La plupart des espèces ne fréquentent qu'un seul ou que quelques-uns de ces biotopes, mais que ces derniers s'interpénètrent, comme les doigts de deux mains jointes se faufilent les uns entre les autres, se traduit par l'abondance et l'extrême diffusion de tels oiseaux de la mouillère que le Canard malard, la Sarcelle à ailes vertes, le Petit morillon (*Anatidae*), la Bécassine ordinaire (*Scolopacidae*), le Moucherolle des aulnes (*Tyrannidae*), la Fauvette jaune, la Fauvette des ruisseaux et la Fauvette masquée (*Parulidae*), le Carouge à épaulettes et le Mainate rouilleux (*Icteridae*), le Pinson des prés, le Pinson de Lincoln, le Pinson des marais et le Pinson chanteur (*Fringillidae*). On n'a pas de données sur la densité sauf pour quelques types de tourbières où elle s'élève rarement à plus de 100 couples par km². Les régions marécageuses plus fertiles permettent probablement la subsistance de populations d'oiseaux bien plus denses.

Les environnements modifiés par l'homme comprennent ceux qu'on a déboisés pour l'agriculture, des emprises, des immeubles, des barages, etc. Si les oiseaux de ces biotopes découverts y fréquentent surtout les vestiges de bosquets ou la lisière des lieux affectés et de ceux qui sont restés davantage à l'état de nature, il en est quand même, comme le Pluvier kildir (*Charadriidae*) et le Pinson des prés (*Fringillidae*), qu'on retrouve à peu près partout. Trois espèces introduites par l'homme, quatre espèces d'hirondelles (*Hirundinidae*), le Merle d'Amérique (*Turdidae*), le Pinson familier et le Pinson chanteur (*Fringillidae*) caractérisent l'avifaune des villes. La densité des couples y est directement proportionnelle au temps écoulé depuis que l'endroit a pris des allures de ville et inversement proportionnelle à la latitude; elle varie de 200 à 600 couples le km². Elle est habituellement au moins aussi élevée que dans le milieu naturel avoisinant mais comporte un nombre d'espèces moindre qu'en terrain boisé.

L'avifaune boréale du Canada comprend des espèces dont l'effectif est à son plus élevé dans la zone boréale, ainsi que d'autres en provenance de la zone avoisinante, surtout des forêts de feuillus et des forêts de transition du sud-est. Il ressort de la structure de la distribution, et de paires d'espèces étroitement apparentées et de sous-espèces, que les principales lignes de rupture de la composition de l'avifaune boréale se trouvent, l'une, le long des Rocheuses canadiennes, et l'autre, entre le lac Supérieur et la baie d'Hudson; d'autres lignes de rupture importantes apparaissent le long de la chaîne littorale de Colombie-Britannique et à travers la partie méridionale du centre de cette province, pour constituer la limite sud-ouest de la zone boréale au sens où je l'entends ici. Peu d'espèces sont confinées à la forêt boréale de conifères et la plupart appartiennent à des familles, des genres ou des espèces qui de toute façon ne quittent jamais le milieu arctique. Le reste est constitué soit d'espèces provenant d'autres biotopes, soit d'espèces qui se font à des forêts très diverses, notamment à des forêts de feuillus de l'est de l'Amérique du Nord dont maintes familles sont originaires.

Plus de 80% de toutes les espèces qui se reproduisent dans la région boréale ou au nord d'elle hivernent plus au sud. En gros, la moitié des espèces terrestres migratrices hivernent au sud du 30°N, dans les zones tropicale ou sub-tropicale. Nous ignorons si la distribution des sujets correspond à celle des espèces. La plupart des espèces qui hivernent dans la zone boréale habitent la forêt boréale toute l'année; les autres appartiennent à la zone de transition sub-arctique et hivernent, tant dans les

aires dégagées à l'intérieur de celle-ci, qu'au nord et au sud de la zone boréale. La plupart des espèces migratrices ne passent dans la zone boréale que de trois mois, cas des insectivores exclusifs, à cinq mois, cas des insectivores qui se nourrissent à l'occasion de graines et de fruits et dépendent donc en grande partie d'aires biogéographiques plus méridionales pour leur survie. Les oiseaux de la plupart des espèces qui habitent en permanence la zone boréale exécutent des migrations en masse à l'occasion desquelles il leur arrive de nicher quand les circonstances s'y prêtent. Dans l'ensemble, les oiseaux de la zone boréale semblent capables de s'adapter aussi bien aux changements graduels de leur milieu lors des époques glaciaires qu'aux changements radicaux d'aire biogéographique à l'occasion des migrations annuelles.

L'effet de l'homme sur les oiseaux de la zone boréale a été bien moindre que dans la plupart des autres aires biogéographiques où il s'est installé, ce qui tend à entretenir la superstition populaire comme quoi les richesses de ces régions sont inépuisables. L'extraction de minerais a bien créé des déserts ici et là, mais jamais jusqu'ici d'assez importants pour mettre en cause l'existence d'oiseaux. L'agriculture, de même, a été presque insignifiante. La tendance au raccourcissement du cycle d'exploitation des forêts pourrait mettre en danger les forêts mûres, surtout, mais, vu le coût du transport, cela ne se fera sans doute qu'en des lieux d'accès plus facile. Les oiseaux dont la présence caractérise les peuplements forestiers climaciques les plus fertiles semblent attachés aux types les plus riches présents dans une région donnée plutôt qu'à un type donné de forêt à travers l'ensemble de leur aire de distribution; mais, les forêts les plus riches seront les premières cibles le moment venu de l'exploitation forestière. Les aménagements hydro-électriques détruisent des collectivités d'oiseaux riverains qui souvent étaient prolifiques, encore que, dans ce cas aussi, la plupart des espèces touchées soient répandues sur une vaste aire ou se prêtent à des biotopes fort variés. Les produits chimiques toxiques mettent en danger un certain nombre de rapaces ou de piscivores: constituant le dernier maillon d'une longue chaîne alimentaire, ils absorbent ces poisons à haute dose. Les écosystèmes du Canada, loin de se suffire à eux-mêmes, sont partie intégrante et d'aires migratoires à l'échelle de l'hémisphère pour les oiseaux et d'un écosystème global assujetti à l'exploitation de l'homme.

Introduction

This study considers the birds of one major biotic region, the northern conifer forest – here termed the boreal region – of North America*. It is not a check-list, annotated or otherwise expanded. Rather, it attempts to suggest the groupings and densities of birds that occur in various biotic and geographic situations within the boreal region. My inspiration stemmed partly from the late R. E. Moreau's *The Bird Faunas of Africa and its Islands* (1966), but the region under study here boasts no more than two avifaunas, and these overlap considerably. I look on this as a new kind of *Birds of Canada*, with Canada considered as the Canadian (ecological) zone of Merriam (1894) and his successors, rather than the political entity of Godfrey (1966). The main fields considered are thus bird communities and bird geography.

The ideas above were enough to spur me to carry out the work which led to this publication. One of my main contentions was that birds of the boreal forest region of Canada had attracted less study, and far less relative to the area of this region, than those of any other part of Canada. This still holds. Early biological explorations, such as those of Richardson, Preble, and Todd, followed closely the start of geographic exploration here, and these continued into the early part of the 20th century. But the flood of detailed studies of birds, whether on nesting biology, behaviour, ecology, or populations, in the last 40 years has largely bypassed the boreal region. If considered at all, it usually has been represented only by studies in peripheral areas such as Maine (MacArthur 1958, Stewart and Aldrich 1952), southern Ontario (Martin 1960), Michigan (Kendeigh 1948), or Minnesota, which were convenient of access from American universities with ornithological research groups. The few major bird studies in the main boreal forest region were concerned with birds in areas of forest insect epidemics (e.g., Kendeigh 1947, Morris *et al.* 1958), which are not typical of the state of things there at other times. I spent all or parts of most breeding seasons from 1957 through 1975 in the conifer forest regions of Canada, including eight summers devoted to systematic quantitative studies of birds, and have accumulated a lot of new data as well as some new ideas about arrangements of existing information.

Not least among the justifications for this work must be the rapidly increasing exploitation of heretofore ignored areas of Canada. Concern has been aroused especially by the potential destruction of the fragile tundra biome and the disregard of native peoples who depend on northern environments. But the "Roads to Resources" program (Department of Indian Affairs and Northern Development 1960), the "Mid-Canada Corridor" proposal (Acres Research and Planning Ltd. 1967), the Nelson–Saskatchewan rivers diversion (Saskatchewan–Nelson River Basin Board, Regina, 1972), and the James Bay power project (Bourassa 1973) all have had or would have drastic effects on the boreal region rather than the Arctic. Such proposals continue to appear. Man's potential for totally altering his environment must not be underestimated, as exemplified by *The hardwood forests that vanished* (Edwards 1969) in southern Ontario. The evidence, accumulated over three centuries in Canada's eastern provinces, is that much of the boreal region is more productive left as a natural place for trees to grow than put to other uses.

All new northern developments are absolutely dependent on abundant, cheap energy, to make settlements and industries feasible through the northern winters. Without detailed information about these areas, conservation proposals to minimize or oppose developmental damage are flawed from the start, as it is not possible to obtain useful biological data in a brief visit just before the snow flies or the bulldozers move in. This study provides some baseline data against which the impact of developmental proposals may be assessed. It is not and never can be complete, but it is a clear advance on what was previously available from this region.

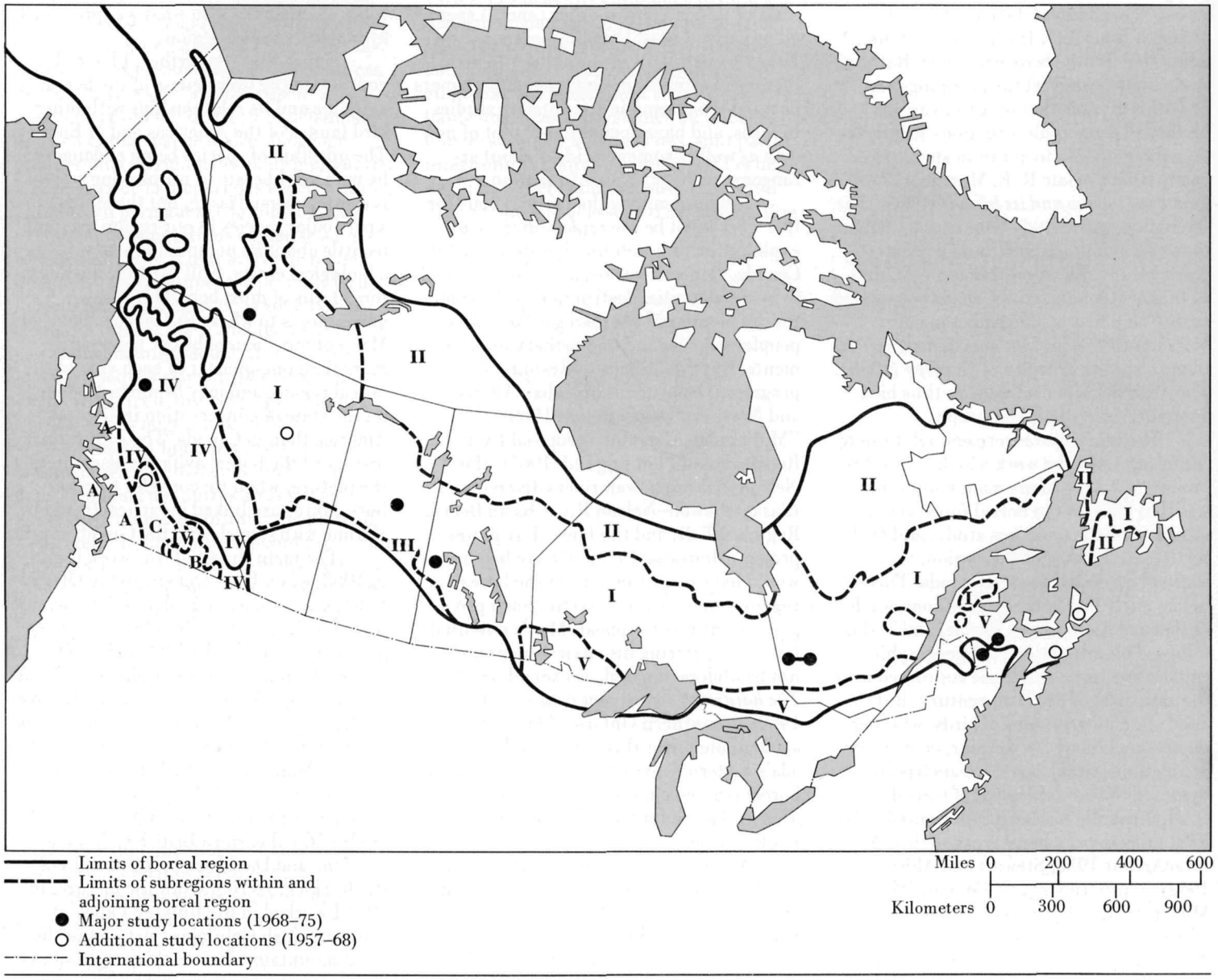
Going one step further, I have also considered the uniqueness of the boreal avifauna and its relationships with other bird faunas of the Americas and of Eurasia. The question of species being endangered by man's deliberate or unthinking actions is a controversial issue, but the status of a particular species in our region may tell us little about its potential for survival as a biological entity. Still further, the migratory status of most boreal birds raises questions as to where the real problems lie. Many of our "boreal birds" spend little more than one-quarter of each year in the boreal region, and may be more dependent on the state of conservation in Central America than in Canada. The evolutionary history of the boreal avifauna also enters the picture, when we consider whether boreal birds are linked inextricably and for all time with Canada and the Canadian zone.

The main thrust of this work began in 1968, when I was transferred to Ottawa to work on non-game bird populations, my work for the previous decade having been primarily on ducks. In 1968 and 1969, I carried out bird census studies in central New Brunswick, and in 1970 and 1971 my work was in the Clay Belt of central Quebec and Ontario. Moving westward, I worked in western Manitoba in 1972 and in central Saskatchewan in 1973, followed by the summer of 1974 in the Fort Nelson lowlands of northeastern British Columbia (Erskine and Davidson 1976) in sight of the Rockies. To round out the picture, in 1975 I worked in the Bulkley Valley of central British Columbia, just east of the coast mountains. Before this period of intensive study, I had studied birds in summer near Halifax, N.S. (Erskine 1957), in western Cape Breton Island, N.S., in 1960 through 1968 (Erskine 1971*b*), in the Peace River–Slave Lake region of Alberta in 1964 (Erskine 1968*a*), and in the Cariboo–Chilcotin district of British Columbia in

* This region is termed "taiga" by many writers, but some restrict this term to the forest-tundra ecotone. To avoid confusion, I have avoided using "taiga" at all.

Figure 1
Approximate limits of the boreal region as discussed in this report; modified from Munroe (1956) and Rowe (1959)

Figure 1



1958 and 1959 (Erskine and Stein 1964). Data from these regions, though only qualitative, helped to round out the picture. Locations of major and additional study areas are shown in Figure 1.

Other major sources of information recently compiled were the catalogue of bird census plot studies in Canada (Erskine 1971*a*, 1972, 1976), and the data from the co-operative Breeding Bird Survey (Robbins and Van Velzen 1967, 1969; Erskine 1970*ff*.). These were especially helpful for areas which I had not visited, although they share with all earlier sources the bias toward well populated areas.

The mapping method (International Bird Census Committee 1970) was used in deriving density figures for various habitats, despite the inevitable differences in interpretation between observers (Best 1975, Svensson 1974). Such differences are the more important the smaller the study areas surveyed. By using plots of at least 16 ha (40 acres) in area, I believe that difficulties in comparisons among my own samples are minimized, although even here the lower densities tend to be overestimated (Erskine 1974*b*). Inclusion of my data in the comparisons wherever possible helped to show where generalizations were feasible. The availability of several samples of most types made comparisons much easier, since marked discrepancies quickly became obvious. My interpretations of census data seem more conservative than many others, not least because I require that a cluster include observations spanning at least two weeks, with at least three registrations included, to be counted as a territory. My use of large study plots also contributes to lowering the density figures found (Oelke 1966).

Most criticisms levelled at the mapping method in a recent review by Berthold (1976) are accurate but unhelpful. No alternative method proposed by Berthold is both accessible to the interested but unaided volunteer and practicable on the extensive scale needed in North America. Intensive population research on small areas is needed too, but we do not have the manpower or the money to cover our subcontinent at that level of thoroughness in time to be of any help to conservation in this century. Mapping methods are so far superior to strip or transect counts in comparability of results between observers, and even farther in advance of the qualitative assessments of earlier generations, that we would be foolish to pass up such methods because they are imperfect, as we well know.

One obvious imperfection, however, is the inadequacy of habitat descriptions for many bird censuses, particularly when such descriptions are confined to numerical comparisons of major tree species. The intrusion of a different habitat, making up 10% or less of the total area, may introduce one or more major bird species and several minor ones which have nothing to do with the habitat represented by the general description. The method of James and Shugart (1970) is an improvement over the previous variety or lack of systematic habitat data presented, but it is no substitute for a verbal description of a study area in each report. It is probably more helpful for comparing plots within a particular habitat type (e.g., one pine plot with another pine plot) rather than between types (e.g., a pine plot with one in spruce).

The Breeding Bird Survey data have no information on habitats, although I often have noted in general terms the habitats at each stop in the course of these surveys. Nevertheless, they do provide standardized sample counts from many areas unrepresented by census plot data, and may thus be used in a broad distributional survey. Since they provide index counts, not merely recording presence or absence, they are more valuable for mapping ranges than would be a comparable number of lists with no indication of numbers (Erskine 1971*c*).

The numbers of species found in samples are treated very cautiously. Despite the vast literature on diversity indices derived from numbers and densities of "breeding species" found on census plots, I remain sceptical both of their validity and their usefulness. Many species detected during censuses are accepted or rejected as "breeding birds" by quite arbitrary decisions which would be reversed by another worker using the same data. This is not to deny that more species will be found in one region or one habitat than another. But such differences are better assessed from careful comparisons of many samples from each group, rather than the varying chances of detection and the subjective interpretations associated with most individual studies. Many scarce species can only be evaluated adequately by special studies, rather than by the kind of broad overview given by general censuses, and this is one reason for the cursory treatment of many non-passerine groups in this presentation.

Parallel criticisms can be levelled at calculations of avian biomass for various habitats. The larger, non-passerine birds, which are less accurately determined by the standard mapping censuses, influence the biomass to a much greater extent than they do the numbers of species or the total density. A rough calculation suggests that grouse and raptorial birds, which make up not more than 2% of the total density, may comprise 35 to 50% of the avian biomass. Even small over- or under-estimates of their numbers would greatly bias any biomass calculations, so none have been attempted.

Before discussing the communities of the boreal region, I will consider the boreal ecosystem as an environment for birds.

The northern forest biome

1. Environment

Munroe (1956) produced an excellent summary titled *Canada as an environment for insect life*, much of which is relevant but does not need repeating in full here. We are concerned with the Canadian boreal forest biome as an environment for boreal birds, so other biomes require consideration mainly as differing types lying beyond the limits of the boreal region. We are here considering rather more than half the area of Canada (Fig. 1), omitting the treeless areas of the north and the south, and the areas of mainly broad-leafed forests in the southeast. This vast area forms a band of about 10° latitude north to south and extending from Newfoundland to Yukon Territory (long. 53°W to 141°W), roughly 6.5 million km² (2.5 million mi²). All except a small, northwestern part of Canada's boreal region was completely ice-covered during the Pleistocene glaciations. A little over 100 tree generations have passed since vegetation first colonized the area after the ice and the post-glacial lakes disappeared (Boughey *in* Baldwin *et al.* 1962). All of Canada's boreal forest birds must be still more recent immigrants. The birds of this region are influenced both by their physical and biotic environment.

1.1. Terrain and water

Bedrock geology scarcely influences the life of birds directly, though its contribution to topography and soils undoubtedly has indirect influence on the vegetation and thus the birds. Even structural geography has little direct influence, but a few examples deserve some mention.

a. The irregular terrain of the mountainous regions of western North America has a profound influence on local climate and vegetation. The series of parallel mountain ranges, trending from northwest to southeast, shut off almost completely any maritime influence from the interior plains, while valleys between the ranges differ greatly both from the coast and the plains. Although there is a major avifaunal divide roughly along the line of the Rockies, at the east edge of the mountain region, this probably is related to the evolutionary history of the recolonization of these areas following deglaciation, rather than to the mountains acting as a barrier to dispersal.

b. The presence of Hudson Bay, a large expanse of water almost in the middle of Canada and now largely ice-covered for nine months of the year, also influences the climate of surrounding areas immensely, pushing the borders of the subarctic south of 55°N. This cool, maritime region probably also influenced the development of the Labrador ice-sheet of glacial times, around whose margin (when it was thawing) the glacial lakes Barlow–Ojibway and Agassiz gave rise to the plains of the Clay Belt of Quebec and Ontario, and of southern Manitoba respectively.

c. Still farther east, the Gulf of St. Lawrence and connecting channels open a vast gap where the easternmost part of the boreal forest region might have been expected to lie. This latitudinal belt of vegetation here is greatly fragmented, as well as being exposed to maritime influence far in from the open ocean.

1.2. Climate

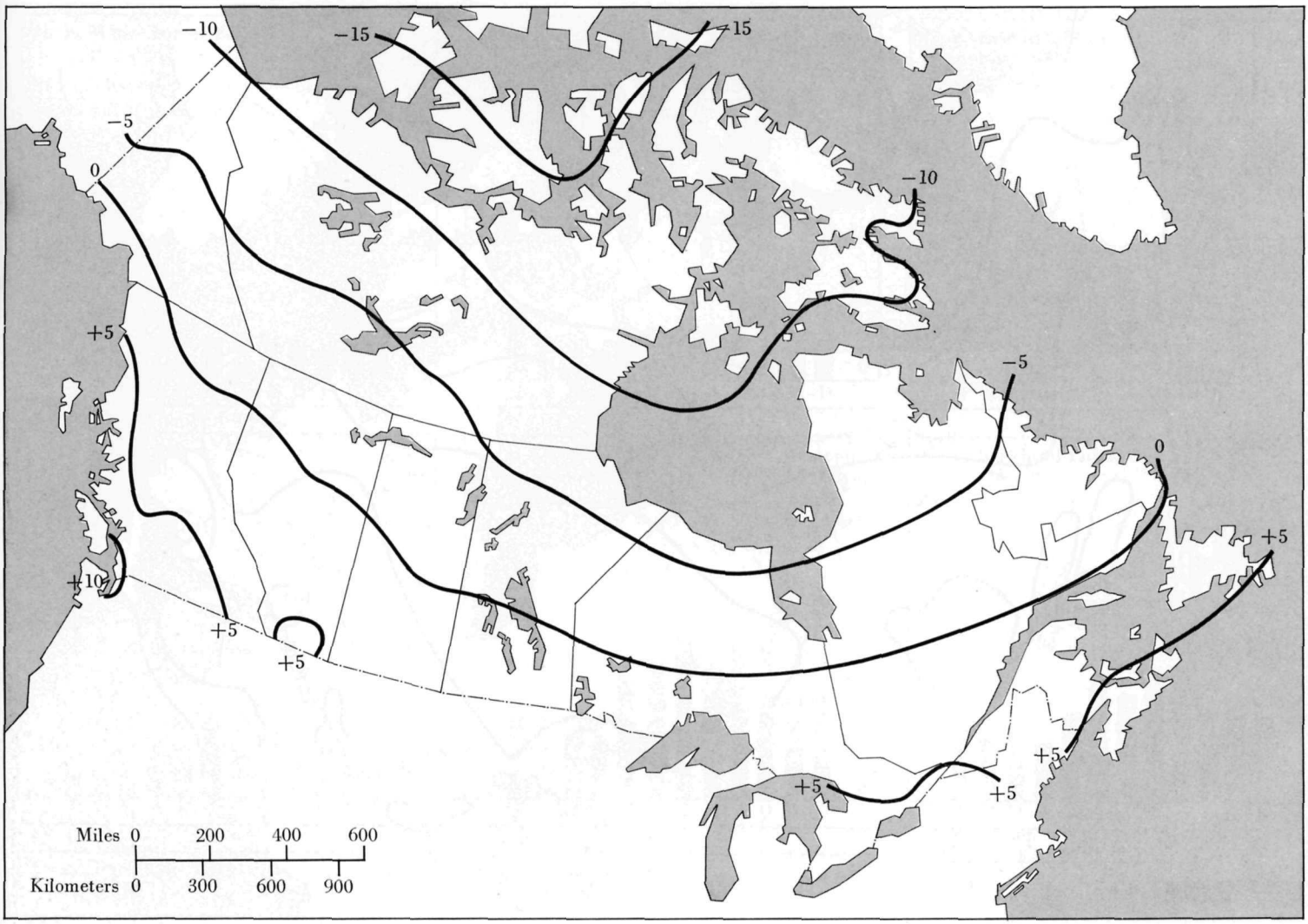
The climate of boreal Canada is thus much influenced by geographic features. In broad terms, the boreal region lies between the mean annual isotherms of +5° and −8°C (+40° to +20°F) (Fig. 2a), but the annual precipitation varies much more, some areas having less than 40 cm (16 in.) and others at least three times that amount (Fig. 2b). The western mountain ranges show an alternation of wet, west-facing slopes and dry, east-facing slopes, all becoming progressively less wet with increasing distance from the Pacific Ocean. Many of the dry areas in the rain shadow of the mountains in southern British Columbia receive too little precipitation to support forest cover, under prevailing temperatures, and the same holds for the prairie region. To the north, lower temperatures, and to the east, increasing precipitation allow the development and continuation of forests in such situations. The cooling influence of Hudson Bay leads all the isotherms in a southeastward direction until east of longitude 80°W. Precipitation generally increases all the way eastward from the Rockies to the Atlantic coast. All parts of the boreal region are snow-covered in winter, at least from November to April and often longer, when all waters except the most rapid are closed by ice. The summers are often warm, with over half of all precipitation falling in the growing season. Areas downwind from Hudson and James bays may experience killing frosts until the ice cover in these basins breaks up, usually in mid-June or later, whereas western areas are more equable in summer. Bryson (1966) has suggested from analysis of air streams and frontal positions that the boreal forest region east of the Rockies occupies that area dominated by Arctic air in winter and by Pacific air in summer; i.e., "between the . . . modal southern boundaries of Arctic air in winter and in summer." The climatic uniformity of the region is exemplified by Figure 3, which shows monthly mean temperatures and precipitations for selected weather stations in the northern and southern parts of the region across Canada. Slight, but consistent, differences within the region include the lower winter temperatures in the Prairie Provinces (Fig. 3c, d), the progressively later periods of winter minimum and summer maximum temperatures as one moves east, the general precipitation increase towards the east coast, and the more pronounced dry and wet seasons (wettest month[s] with 2–3 times the precipitation of the driest month[s]) in the west and especially in the Prairie Provinces.

1.3. Vegetation

Vegetation is under the influence of substrate and topography as well as climate. Since all animal life depends ultimately on plant life for its existence, terrestrial biotic communities are customarily defined by their climatic climax vegetation. Here we are considering the birds of the northern

Figure 2a
Mean annual temperature (°C); modified from Munroe (1956)

Figure 2a

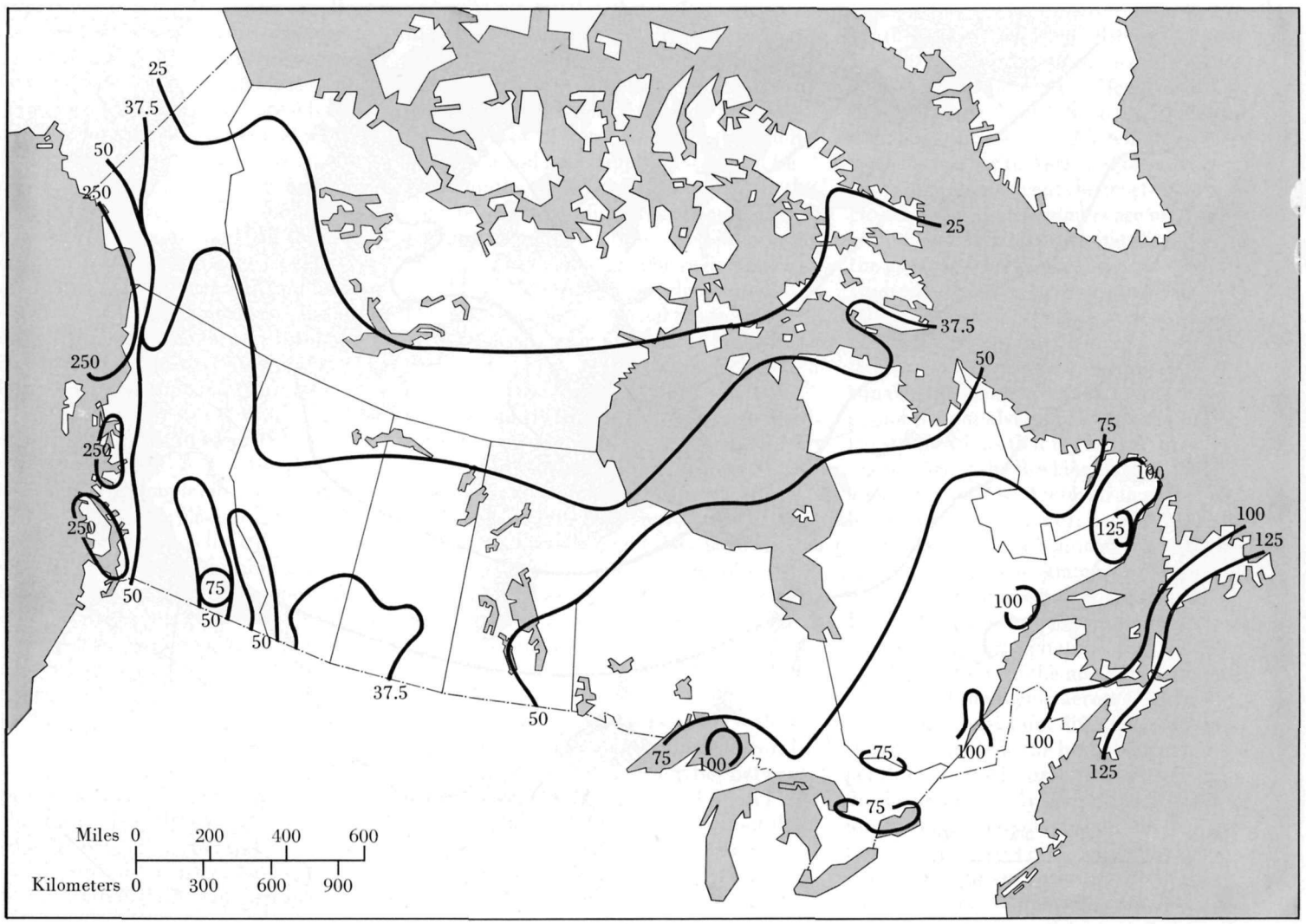


conifer, or "spruce–moose", biome (Fig. 1), a major vegetational formation which stretches across North America, Europe, and Asia. This region is characterized by a climax vegetation of needle-leafed trees, including particularly spruces (*Picea*) and firs (*Abies*), with pines (*Pinus*) important in successional stages (LaRoi 1967). At the climax, there is little understorey other than regeneration of canopy species, but there is a dense ground layer of low, evergreen shrubs (*Vaccinium*, *Ledum*) and mosses (*Pleurozium*, *Hylocomium*, *Hypnum*).

On the west coast of North America, much greater precipitation and milder winters have allowed development of a temperate rain forest (Fig. 1–A) dominated by hemlocks (*Tsuga*) and cedars (*Thuja*), with abundant understorey and shrub layers and ferns. Vegetationally this is quite distinct from the boreal forest proper, but its birds differ less from those of other parts of western North America than might be expected. The Columbia Forest of the damp, western slopes of some interior ranges of British Columbia (Fig. 1–B) also shows a hemlock–cedar climax, but is clearly transitional towards the spruce–fir type. The Montane Forest of the dry interior plateaux of southern British Columbia (Fig. 1–C) may be considered a warmer and drier variant continuing south from the boreal forest, with Douglas fir (*Pseudotsuga*)

Figure 2b
Mean annual precipitation (cm); modified from Munroe (1956)

Figure 2b

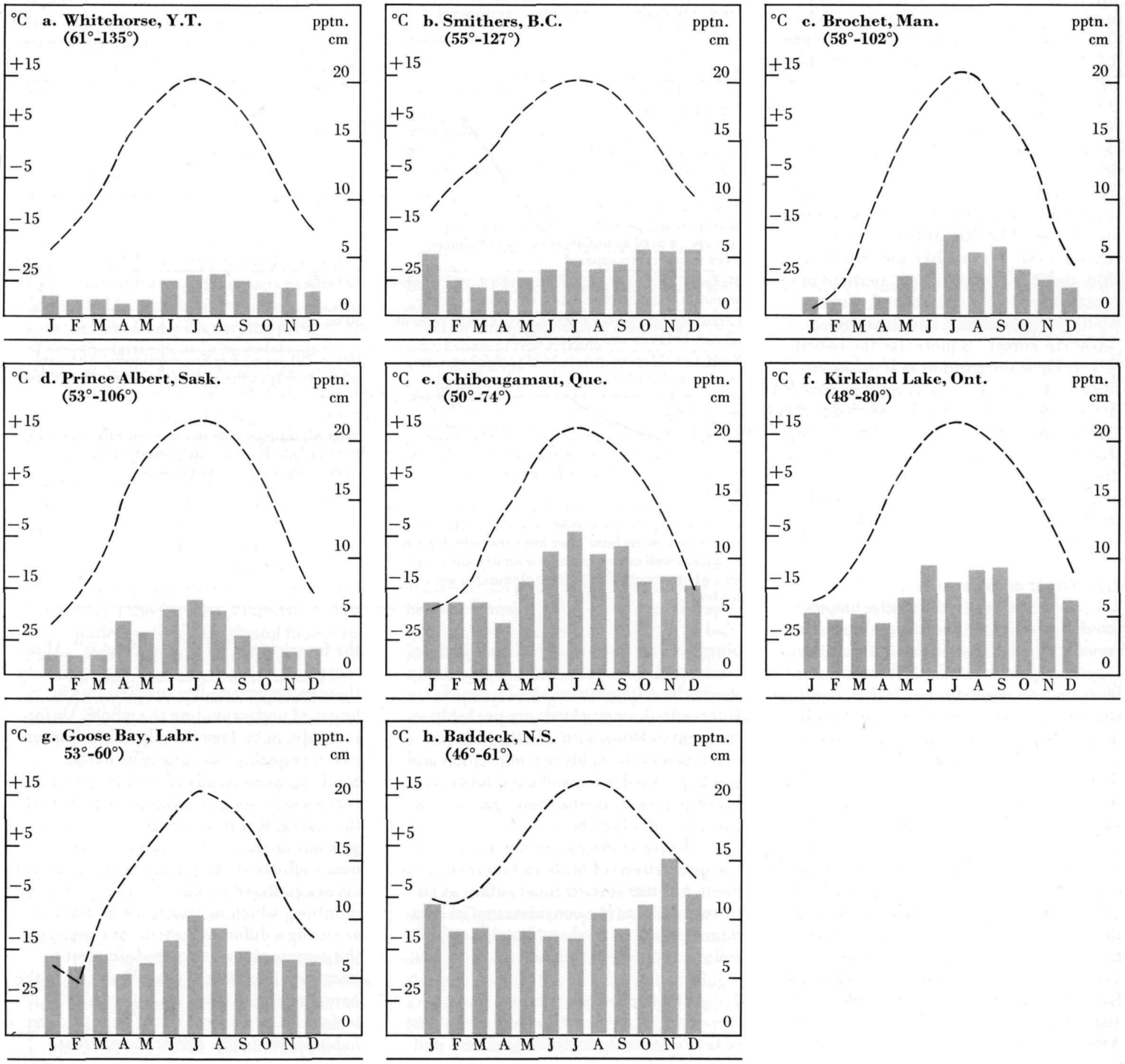


replacing spruce and fir. The Subalpine Forest, occurring at higher elevations along the mountain chains all the way to Mexico (Fig. 1–IV), blends into the boreal forest in northern British Columbia and southern Yukon Territory, though in more southern parts it is characterized by different species of spruce and fir. All of these are basically needle-leafed conifer climax areas, and all will be considered to some extent in subsequent discussion; but the Coast, Columbia, and Montane forests (Rowe 1959) are not considered here to be parts of the boreal region (Fig. 1).

The main boreal forest (Fig. 1–I) extends from southern Yukon Territory (valleys only) across northern British Columbia and southern Mackenzie, eastward and southward past James Bay to the Gulf of St. Lawrence. To the north it grades into the treeless arctic tundra through a wide, subarctic ecotone (Fig. 1–II) where local conditions allow an interdigitation of forested, shrubby, and open areas. To the south, once the Rockies are passed, a similar but narrower area of intergradation with the treeless prairie (Fig. 1–III) occurs, now much altered by human intervention. As precipitation increases eastward, tree cover again becomes possible, and from Manitoba to the Atlantic coast the adjacent formation southward is a forest dominated by broadleafed trees — "Eastern Deciduous For-

Figure 3
Mean monthly temperature (dashed line) and precipitation (histogram) for selected weather stations in the boreal forest region (data from *Monthly Record of Meteorological Observations in Canada*, Atmospheric Environment Service, Environment Canada)

Figure 3



ests" (Braun 1950) = "Nemoral Zone" (Sjörs 1963). Here, too, is an area of intergradation (Fig. 1–V) — "Hemlock–White Pine–Northern Hardwoods Zone" (Braun 1950) = "Boreo–nemoral Zone" (Sjörs 1963) — which in Canada has been termed the "Great Lakes–St. Lawrence and Acadian forest regions" (Rowe 1959). These are certainly broader than the ecotone from prairie to forest, but narrower than that from tundra to forest, and they are clearly transitional mixtures of conifer and broad-leafed trees. The "Great Lakes–St. Lawrence Forest" is more like the strictly deciduous forest farther south, perhaps because these share a continental climate, whereas the maritime, and thus cooler, "Acadian Forest" is more like the boreal forest. Their recognition as separate entities is at least partly because they covered the longest and most thickly settled parts of Canada and have thus received more study than the rest. Finally, the conifer forest is limited at high elevations in the western mountainous areas, where it grades into treeless alpine meadows and rock or gravel slopes.

Table 1
Succession after fire or clear-cutting on fairly level, well drained (zonal) sites – xerosere of boreal forest

Successional stage	No. of yrs after fire
Fire-blackened snags with bare soil or scattered herbs between them	0 to 5*
Snags with herbs, small shrubs, and seedlings or sprouts of pioneer trees – jack pine, or trembling aspen, or paper birch (depending on the previous cover)	3 to 15
Few snags & stubs (others fallen) with dense growth of shrubs and small trees of pioneer species – if seed available, seedlings of climax trees may start to appear†	10 to 40
Medium-sized trees of pioneer species, with varying amounts and ages of climax trees in their shade	25 to 75
Large trees of pioneer species, with climax trees of all ages between and in their shade	50 to 150
Scattered old trees and stubs of pioneer species amid mixed-aged stand of climax species, with occasional younger trees of successional species in openings	100 to 250 years after fire, continuing with variations mainly in the ages of the oldest climax trees.
* The spread of dates given reflects not only the duration of a recognizable stage in succession but also the variation in growth rates with latitude, altitude, and exposure.	*Note:* All time periods will be somewhat shorter on more favourable sites, and longer – often far longer – on less favourable ones.
† The time of appearance of climax tree species varies with the availability of seed as well as with the site conditions, being later after hot fires (which burn humus as well as vegetation) or on dry sites, and also where repeated fires have eliminated seed sources.	

1.4. Other animals

Among the other biotic factors influencing birds are other animals, which function as predators, competitors, and especially prey, of birds. Although many birds feed on vegetation — leaves, seeds, or fruits — at some time of year, nearly all depend on animal food as a high-protein source for rapid growth of their newly-hatched young. Insects and other small invertebrates are used by many birds; small vertebrates by a lesser number, and large animals only as carrion (after death). Birds experience competition from other animals, especially the smaller mammals, for food and shelter, the latter chiefly among birds that nest or shelter in cavities. Predators on birds include members of all classes of vertebrates, although fish and amphibians have few opportunities, and reptiles (snakes) prey mainly on eggs and nestlings. Among invertebrates, a few insects (ants, blowflies) are known to feed on flightless young birds. Parasites belonging to many invertebrate phyla may also be noted. Interactions among birds are probably as frequent as those with all other classes combined in the fields of competition and (perhaps) predation, and a few birds are brood parasites, laying their eggs only in the nests of other species.

Whole books have been written on the interactions of birds and their environment, but this section must suffice as an introduction to the consideration of communities within the boreal region, which follows in the next section.

2. Plant communities

Early man marvelled at the wonders of God's creation, including the seas and the forests and "all that in them is". More recently, the tendency has been to classify them into ever smaller subdivisions in hopes of understanding the whole. Unfortunately, in biology the whole is not often exactly equal to the sum of its parts. Studying pure stands of each major tree species may not give a complete picture if the typical forests of a region are heterogeneous mixtures. Furthermore, despite man's efforts at classification, birds are not always confined to one or a few plant communities, which may only mean that they are using a different system for classifying the communities. It seemed simplest to start with five basic types of habitats in the boreal region, namely: conifer (needle-leafed) forests, broad-leafed forests, open habitats, wetlands, and artificial areas.

Also there is a vast array of successional types, which were rather little sampled in this study, but cannot be ignored in an overall summary.

The concept of forest succession involves a sequence of habitats from bare ground or open water to closed, self-perpetuating forest. The latter, commonly termed "climax", varies depending on soils, moisture, exposure, and availability of seed stocks. Some forest ecologists on this basis deny the existence of any climax and even of communities, but most workers find these concepts indispensable. In the boreal forest, climax is typically dominated by needle-leafed trees, usually spruces but often with varying proportions of firs, the latter mainly on better sites (those on well-drained, fairly level areas with adequate soil moisture). Other conifer species occur in successional stages, which may be long-lasting under certain conditions, e.g., pine stands on sandy soil, or tamaracks around bog margins. Whether hemlocks have any part in the boreal forest is questionable, although they form the climaxes in areas of higher relative humidity and more moderate winter temperatures, adjacent to the boreal region in the east and the far west. Likewise, cedars are confined to sites of high soil moisture in the same regions as the hemlocks.

Broad-leafed trees in the boreal region are strictly successional after fire or cutting, or else confined to unstable sites such as river gravels. Where seed sources of spruce and fir have been virtually eliminated over vast areas by repeated fires, with or without cutting, poplar or birch forests may persist over long periods. Maples, excepting one subcanopy species in the east, do not penetrate the boreal region — Canada's maple leaf emblem is representative of only a small part of this country.

Open areas, too, are successional in the region under study. On terrestrial sites they seldom persist except where bedrock is too close to the surface to allow establishment of tree cover. Elsewhere, such areas start to grow up within a decade and become forest within a century. The succession from open water to marsh or bog is far slower, and open bogs or muskegs require many decades or even centuries before progressing to closed forest. Man's artificial areas are only special cases of open areas, deliberately kept at early stages of succession. These last are scarce in the boreal region, where short growing seasons and infertile soils have restricted agricultural possibilities, and where urban communities are small and widely separated.

Table 2
Succession from open water* — hydrosere of boreal forest

Successional stage	Time scale
Open water with submerged aquatic vegetation	Time scale varies greatly with site conditions, including topography, soils, water temperatures
Water areas with emergent vegetation well out from shore	
Wet areas with some standing water and shrubby as well as herbaceous vegetation; the first small tamaracks may appear here†	Probably at least several hundred years from open water‡
Damp areas (water shows only when surface mat is depressed) with shrub and moss hummocks and well-spaced small trees – tamaracks or black spruces	Perhaps 10 to 100 years‡ from previous stage, depending on precipitation cycles and drainage
Damp areas with low forest of tamaracks or black spruces	Perhaps 20 to 50 years from previous stage, unless halted by rising water table
Dense, medium-aged forest of black spruces, with some balsam fir regeneration	Perhaps 25 to 75 years from previous stage
Mature black spruce forest with some younger balsam firs of varying ages	Perhaps 25 to 75 years from previous stage

* These stages are most often recognized as concentric zones around the edges of a depression or strips along the edges of a slackwater stream; except for very small depressions, this sequence need not be viewed as inevitable.

† The outline given is for bogs with virtually no lateral water movement; along slow-moving streams, better drainage near the banks may allow intrusion of poplars and later of white spruce, although the typical bog succession may occur farther from the open water.

‡ The time scales given are little more than educated guesses.

Brief outlines of the main types of succession in vegetation of the boreal region will place in perspective the communities which have received appreciable study. Tables 1 and 2 respectively show the succession after fire or clear-cutting and that from open water, with a rough idea of the time scales. Thus, climax spruce or fir stands are seen to be usually of mixed ages, and often with considerable admixture of poplar or birch from earlier successional stages and from growth in openings. Moreover, it is rather unusual for boreal areas to survive for 100, let alone 250, years without a fire, and still less usual for such a period to elapse without forest insect outbreaks; so true climax stands are few and far between (Baldwin *et al.* 1962).

In selecting my study areas, I sometimes drove several hundred miles to find even one stand of mature firs. Such stands may be climax, but they are not very typical except in the Maritimes (La Roi 1967). On the other hand, mature black spruce on poorly drained soils covers vast areas in some parts of the boreal region. Jack pine is successional on sandy soils, and was usually easy to locate, since roads often follow dry, well-drained ridges and eskers. Aspen stands, another successional type, presented little difficulty except in the

Birds of the boreal region

Maritimes, where fir growth was so rapid as to fill in most aspen forest before the latter had even developed a high canopy (La Roi 1967). Balsam poplar formed pure stands only on river gravels, so large areas were rare. Tamarack, too, was largely peripheral to bogs and thus in small blocks. I did little work in the early stages of terrestrial succession, where most stages are quite transitory and often difficult to work in, but I studied a number of bogs early in the hydrosere. Although both plant and animal succession have been extensively studied in the eastern broad-leafed region (e.g., Kendeigh 1948, Johnston and Odum 1956, Martin 1960) succession has received little attention in the boreal region. My typical program each field season was to census one plot each in spruce, fir, pine, poplar, and wetland, and one in an artificial habitat. If any of these were unavailable within working distance of the rest, some other habitat was substituted, and I made no attempt to replicate plots with a local area.

Bird density data for nearly all plots available for this compilation have been summarized in the census plot catalogue for Canada (Erskine 1971*a*, 1972, 1976), and most have already been published elsewhere.

1. Conifer forests

The northern conifer forest is the essence of the Canadian Zone of Merriam (1894). Certain birds are confined to these forests, and others are most frequent or attain higher densities there without being restricted to them. Much of the early work in categorizing birds as being of this or other communities stems from Kendeigh (1946, 1947, 1948) and his associates (e.g., Martin 1960, Gillespie 1960). Their work was largely in areas peripheral to the boreal forest proper, and like mine was based largely on scattered studies of short duration. Nevertheless, many of their conclusions have stood up in the light of the more extensive data now available.

Many birds occur almost throughout the boreal conifer forests, with little regard for the tree species dominating the community, but there are consistent differences between the birds in the various conifer communities. Some of these differences relate to forest succession, and Kendeigh (1948) recognized a *Zonotrichia–Oporornis* (White-throated Sparrow–Mourning Warbler) forest-edge biocies distinct from his *Dendroica–Regulus* (Black-throated Green Warbler–Golden-crowned Kinglet) needle-leafed forest biociation, both in the boreal forest region. Other differences relate to geographic distribution of various forms, which may reflect post-glacial evolution (Mengel 1964). Still others reflect mainly the degree of disturbance by man or fire or forest insects of the succession towards the biogeoclimatically influenced climax. Finally, some may reflect only our still very incomplete sampling of the boreal forest region.

1.1. Spruces

If any one coniferous forest community can be said to be the typical climax of this biome in Canada, it must be that dominated by spruces, and particularly by black spruce. In the peripheral regions, where most of the pioneering studies were made, this was commonly looked on as a bog forest, late in the succession from open water to forest, but in the vast sweep of forests from Ungava round to Yukon, this is by far the most widespread of all climax forest types. On better drained sites, white spruce may also be present, and with increasing fertility balsam fir as well, particularly in the east, but in all the moister sites black spruce remains as climax. The succession from spruce–fir to hardwoods to hemlock outlined by Kendeigh (1948) and Martin (1960) is only characteristic of the transition zone along the southern borders, as hemlock, white pine, sugar maple, beech, and yellow birch all reach their northern limits before the main boreal forest is reached (Forestry Branch 1950, Sjörs 1963).

The bird species typical of the black spruce community are few, and even these dwindle gradually to the west and north. Most species of the "hard core" persist through many or most of the boreal conifer communities, and these may be looked on as the most typical boreal birds (Table 3):

> Spruce Grouse, Northern Three-toed Woodpecker, Yellow-bellied Flycatcher (E of 95°W), Canada Jay, Boreal Chickadee, Brown Creeper, Winter Wren (E of 90°W), Swainson's Thrush, Golden-crowned Kinglet, Ruby-crowned Kinglet, Nashville Warbler (E of 105°W), Magnolia Warbler (E of 90°W), Myrtle Warbler, Slate-coloured Junco, Chipping Sparrow (W of 90°W), and White-throated Sparrow (E of 95°W).*

To these one may wish to add Hermit Thrush which, however, in the main boreal forest is confined to more open stands (bog forest, disturbed or young successional forests), where it typically replaces the Swainson's Thrush. Along the subarctic border, where open stands are the rule, the Hermit Thrush, with Gray-cheeked Thrush and Blackpoll Warbler, is also a regular member of the black spruce community. Kendeigh's (1948) choice of species to represent the needle-leafed forest biociation seems inappropriate at least for boreal spruce, where the ubiquitous and dominant

* Scientific names listed in Appendix 4.

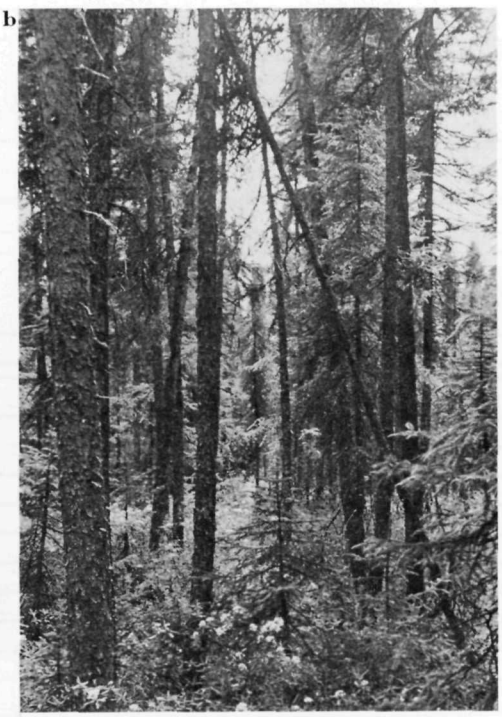
Plate 1

Black spruce, usually in almost pure stands, is the most characteristic and widespread forest type in the boreal region of Canada. Note the lack of understorey other than regeneration, and the dense ground cover of ericaceous shrubs and of mosses — a) bog forest (New Brunswick); b) disturbed middle-aged stand (Quebec); c) dense middle-aged stand (Manitoba); d) mature mixed-age stand (Saskatchewan).

Plate 1

a

b



c

d

Table 3
Summary of data from bird censuses in spruce stands. Each entry gives (arithmetic mean) density in males (or females) per km², followed by the number of plots in that area on which the species was found. The total number of plots summarized is given in the column headings, with the number censused by me in square brackets. References to sources are elaborated in Appendix 1, referring to Erskine (1971*a*, 1972, 1976)

	Age and area											
Species	Young or low (4) N.S.–Ont. [1] no budworm		Medium-mature (5) Que.–NW Ont. with budworm		Medium-mature (2) Ont. [1] no budworm		Medium-mature (2) Man–Sask. [2] no budworm		Mature (5) S Mack.–NE BC [2] no budworm		Low, subarctic (7) Mack.–Man. no budworm		Mature, disturbed (4) central B.C. [2] no budworm	
Spruce Grouse	+	(1)	3	(2)	7	(1)	+	(1)	7	(2)	1	(4)	+	(1)
Northern Three-toed Woodpecker					3	(1)			3	(4)	1	(4)		
Yellow-bellied Flycatcher	16	(3)	3	(2)	30	(2)					2	(1)		
Hammond's Flycatcher													11	(2)
Canada Jay	2	(2)	6	(4)	2	(1)	4	(2)	6	(4)	4	(5)	4	(4)
Boreal Chickadee	5	(3)	9	(3)	4	(1)	5	(2)	10	(5)	5	(5)		
Red-breasted Nuthatch	2	(1)	17	(5)	5	(1)			2	(1)			8	(3)
Brown Creeper	+	(1)	9	(4)	9	(2)	2	(2)					3	(1)
Winter Wren	11	(3)	11	(4)	13	(2)	1	(2)					8	(3)
American Robin	2	(1)	5	(1)					2	(1)	10	(5)	12	(3)
Hermit Thrush	14	(4)	1	(1)	7	(1)					4	(2)		
Swainson's Thrush	12	(3)	32	(5)	10	(1)	16	(2)	39	(5)	12	(5)	38	(4)
Gray-cheeked Thrush											9	(6)		
Golden-crowned Kinglet	17	(4)	48	(5)	13	(2)	10	(2)	5	(2)			46	(4)
Ruby-crowned Kinglet	14	(3)	8	(3)	24	(2)	30	(2)	28	(5)	6	(5)	36	(4)
Solitary Vireo	6	(2)	20	(5)			5	(1)	7	(1)	1	(1)	4	(1)
Tennessee Warbler			34	(4)			30	(2)	30	(4)	2	(1)	12	(2)
Nashville Warbler	27	(4)	27	(5)	50	(2)	11	(1)						
Magnolia Warbler	36	(4)	8	(5)	39	(2)					+	(1)	22	(2)
Cape May Warbler			38	(5)			8	(1)						
Yellow-rumped (Myrtle)* Warbler	25	(4)	24	(5)	20	(2)	32	(2)	55	(5)	21	(7)	12	(3)*
Townsend's Warbler													20	(2)
Bay-breasted Warbler	2	(1)	49	(5)			5	(2)	3	(1)				
Blackpoll Warbler	1	(1)									14	(6)	17	(2)
Palm Warbler	7	(2)							1	(1)	3	(2)		
Common Yellowthroat	29	(4)			2	(1)	3	(1)					2	(1)
Purple Finch	2	(2)	10	(5)	4	(2)							3	(1)
Pine Grosbeak											3	(4)	1	(1)
Pine Siskin			9	(3)	2	(1)	4	(1)					12	(4)
Northern Junco	15	(4)	19	(5)	7	(2)	8	(2)	39	(4)	28	(7)	27	(4)
Tree Sparrow											8	(3)		
Chipping Sparrow			12	(2)			12	(2)	49	(5)	6	(3)	3	(3)
White-crowned Sparrow											7	(4)		

cont'd. on page 21

Table 3 *cont'd.*

Species	Age and area						
	Young or low (4) N.S.–Ont. [1] no budworm	Medium-mature (5) Que.–NW Ont. with budworm	Medium-mature (2) Ont. [1] no budworm	Medium-mature (2) Man–Sask. [2] no budworm	Mature (5) S Mack.–NE BC [2] no budworm	Low, subarctic (7) Mack.–Man. no budworm	Mature, disturbed (4) central B.C. [2] no budworm
White-throated Sparrow	55 (4)	19 (5)	86 (2)	2 (1)	2 (1)	1 (2)	2 (1)
Fox Sparrow						5 (4)	
Overall mean density (range)	370 (270–468)	486 (245–765)	394 (232–556)	193 (174–212)	316 (106–575)	175 (55–240)	469 (134–786)
Reference numbers (to Appendix 1)	I: 65, 69; II: 121; III: 196	I: 57, 94; III: 163	I: 65; II: 126	III: 166, 174	I: 100, 101; II: 8; III: 178, 179	I: 41; II: 8; III: 191 IV: Ebel *et al*	I: 50, 104; III: 223, 224

* Except Audubon's Warbler in central B.C.

Table 4
Approximate numbers of species of breeding birds on census plots of average size* in various habitats in and south of boreal forest in Canada

Dominant tree in habitat	Approx. no. species	
	E of long. 95°W	W of long. 95°W
Spruces	15–20 (no budworm) 20–25 (with budworm)	10–15 8–12 (subarctic or subalpine) 15–20 (W of Rockies)
Balsam Fir	20–30 (no budworm) 25–30 (with budworm)	15–20
Eastern Hemlock	20–25	
Eastern White and Red Pines	15–20	
Jack and Lodgepole Pines	10–15	7–10
Tamarack	15–20	
Poplars and Birches	15–20	12–18 (upland) 20–25 (floodplain)
Maples and Beech	12–20	
Bogs	4–6 (open peat) 7–10 (sedges & shrubs) 9–15 (shrubs & low conifers)	

* Most plots were of 10–20 ha (25–50 acres) in size. The number of breeding species detected rises towards an upper limit as plot size increases (Oelke 1966); increasing tye number of surveys of a plot in a season has a similar but smaller effect (Erskine 1974*b*).

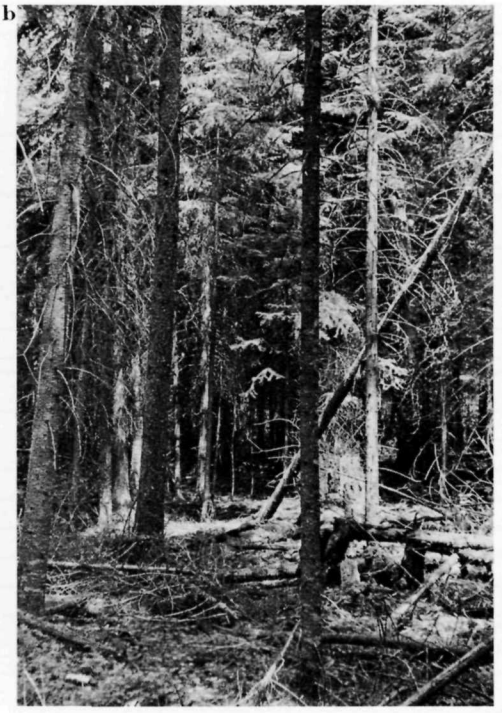
birds are Swainson's Thrush, Myrtle Warbler, and Northern Junco.

Other species often cited as characteristic of needle-leafed forests of the boreal region are more restricted than those above. Some are regular in spruces only in the presence of spruce budworm, Cape May and Bay-breasted Warblers being well known in this context, and Red-breasted Nuthatch also showing this association. Others are associated with a broad-leafed element, particularly in the understorey vegetation, Solitary Vireo and Tennessee Warbler being in this category.

This spruce community is not a particularly rich habitat either in variety of species (Table 4) or in total productivity, whether of vegetation or (presumably) of animal biomass. Total bird densities encountered have mostly been in the range from 150 to 450 pairs per km², decreasing to north and west within the region. The presence of spruce budworm is often accompanied by a few extra species and by much higher bird densities, usually 300 to 700 pairs per km². Intrusion of other habitats into the sample area may also increase the variety and density found. Nevertheless, both drier (pine) and wetter (bog) habitats in the boreal forest support still lower densities, while the richer sites with their higher bird populations are scarce. Balsam fir is typically dominant in such

Plate 2
Balsam fir dominates the climax forest of Canada's boreal region, given adequate drainage and a sufficient period without fire or other disturbance. Note the mixed-age stands, including spruces, poplars, and birches as well as fir, and the varied understorey and shrub layer, with many fallen logs — a) Quebec, b) Manitoba, c) Quebec, d) Saskatchewan.

Plate 2



communities, but except in the Atlantic Provinces this never forms pure stands, almost invariably being accompanied by larger or smaller proportions of spruces and of paper birch or poplars (La Roi 1967). These mixed-species, mixed-age stands offer a much wider choice of niches than does the very uniform black spruce forest, and the birds reflect this clearly (Table 4).

1.2. Fir Stands

Nearly all of the bird species listed as characteristic of the spruce forests are also regular in fir stands, the exceptions being Spruce Grouse and Canada Jay. These are of minor significance in fir, where they are seemingly replaced by Ruffed Grouse and Blue Jay respectively. Densities are roughly parallel in both spruce and fir stands for other bird species regular in both, but a number of other species not often found in pure spruce are characteristic of fir stands (Table 5):

> Red-breasted Nuthatch, Solitary Vireo, Red-eyed Vireo, Tennessee Warbler, Black-throated Green Warbler, Blackburnian Warbler, Bay-breasted Warbler, Ovenbird, American Redstart, and Purple Finch.

Balsam fir becomes rapidly scarcer west of Ontario, with only two western plots, one each in Manitoba and Saskatchewan, censused in this type. Winter Wren, Magnolia Warbler, and White-throated Sparrow extend far to the west in fir stands, though they are almost lacking in pure spruce stands from Ontario to the Rockies. The species added above include those noted previously as associated with spruce budworm (except Cape May Warbler) or requiring a broad-leafed component in spruce stands, plus Red-eyed Vireo, Ovenbird, and American Redstart from the major species characteristic of broad-leafed stands, both in the boreal and northern hardwood regions. The other three warblers (Black-throated Green, Blackburnian, Bay-breasted) are probably the most distinctive species of the fir forest. All are noted for their abundance during spruce budworm outbreaks, which affect fir even more than spruce in the Maritime Provinces, but all are major species in fir even in the absence of budworm. Kendeigh (1946) and Martin (1960) cite Black-throated Green and Blackburnian Warblers as characteristic of hemlock climax stands in the transitional forest south of the boreal forest. The data now available show that these, with the Bay-breasted Warbler in mature stands and the Magnolia Warbler in younger stands, are actually characteristic of the most fertile needle-leafed forest community present in a region. In the Hemlock–White Pine–Northern Hardwoods Region, this is hemlock; farther to the north and far to the northwest, it is balsam fir. Beyond the range of balsam fir, mature white spruces amid poplar stands sufficed in Alberta and northeastern British Columbia (Erskine 1974*c*, Goulden 1974). My work north of Lesser Slave Lake in 1964 (Erskine 1968*a*) also brought out this habitat selection clearly. Upland forests near the roads there were almost entirely of poplars, as repeated fires had eliminated the conifers, but one stand (about 5 ha) of mature spruce and fir produced our only records that summer of eight species — Red-breasted Nuthatch, Winter Wren, Golden-crowned Kinglet, Magnolia, Cape May, Black-throated Green and Bay-breasted Warblers, and Western Tanager.

Breeding bird densities in fir-dominated stands in the boreal region range from 250 to 600 pairs per km² in the absence of spruce budworm, and from 400 to 800 pairs per km² with budworm present. These contain one of the richest bird communities within the main boreal forest, as well as one of the scarcest — except in the Atlantic Provinces. Elsewhere they may deserve more attention, for example, in environmental impact studies, than they have typically received.

1.3. Hemlock and pine

The hemlock and pine communities of the Great Lakes–St. Lawrence and Acadian forest regions (Rowe 1959) serve to link up the boreal forest studies reported here with the earlier, more southern investigations of birds in northern conifer habitats. These forests are transitional between the boreal and eastern deciduous forests in vegetation and also in their birds. We have rather few Canadian samples from conifer communities in this region, most of these being from Algonquin Provincial Park in Ontario (Table 6). The most obvious change from the fir community to that of hemlock stands is replacement of the Boreal Chickadee by the Black-capped Chickadee. A number of other species characteristic of spruce and fir are lacking or very scarce in hemlock, particularly:

> Ruby-crowned Kinglet; Tennessee, Nashville, Myrtle and Bay-breasted Warblers, American Redstart, and Purple Finch.

Conversely, three new warblers appear here, of which Parula and Black-throated Blue Warblers belong primarily to this transitional type, whereas Black-and-White Warblers farther north are confined to broad-leafed forest stands. Most other major species of birds are in common with the communities of northern spruce and fir stands, namely:

> Winter Wren, Swainson's Thrush, Golden-crowned Kinglet, Magnolia Warbler, Slate-coloured Junco, and White-throated Sparrow;

or with the balsam fir community alone:

> Red-breasted Nuthatch, Solitary and Red-eyed Vireos, Black-throated Green and Blackburnian Warblers, and Ovenbird.

Of these, Black-throated Green and especially Blackburnian Warblers often attain much higher densities in pure hemlock stands than in any more boreal types.

Bird densities in hemlock stands were generally higher again than those in fir, with total densities in the range of 500 to 800 pairs per km², which is comparable to all but the richest hardwood stands of the eastern deciduous forest (cf. Webster and Adams 1973). However, most hemlock stands studied in Canada were small and

Table 5
Summary of data from bird censuses in balsam fir dominated stands. Legend as in Table 3.

Species	Area															
	N.B.*–E Que. (2) of total (5) [1] no budworm		W Que.–Ont. (5) [1] no budworm		Man.–Sask. (2) [2] no budworm		N.B.*–E Que. (4) of total (8) with budworm		W Ont. (4) with budworm		very mixed N.B.–Que. (2) no budworm		very mixed Ont. (5) with budworm	
Ruffed Grouse*	+	(1)	8	(5)	+	(1)	7	(4)	2	(2)	5	(1)	6	(4)		
Common Flicker*	+	(1)	4	(3)			+	(1)	5	(3)			5	(3)		
Yellow-bellied Sapsucker*	5	(1)	4	(4)			20	(3)	2	(2)			2	(1)		
Yellow-bellied Flycatcher	12	(5)	6	(4)			9	(6)	2	(2)	30	(1)				
Least Flycatcher	10	(4)	7	(2)			4	(5)	13	(4)						
Blue Jay*	+	(1)	6	(4)			3	(4)	1	(1)	5	(1)	3	(2)		
Boreal Chickadee	7	(5)	2	(2)	3	(1)	6	(6)	11	(4)	5	(1)				
Red-breasted Nuthatch*	1	(1)	3	(3)	8	(2)	6	(3)	17	(4)	5	(1)				
Winter Wren	22	(5)	6	(3)	16	(2)	16	(8)	8	(4)	16	(2)	7	(4)		
American Robin*	10	(2)	1	(2)			12	(2)			21	(1)	16	(4)		
Hermit Thrush*	1	(1)	7	(3)			12	(2)	+	(1)	13	(2)	6	(1)		
Swainson's Thrush	33	(5)	10	(3)			29	(8)	12	(4)	46	(2)	8	(2)		
Golden-crowned Kinglet	6	(5)	16	(5)			15	(6)	28	(4)	21	(2)	3	(1)		
Ruby-crowned Kinglet	18	(4)	12	(5)			12	(7)	4	(2)	21	(2)	14	(5)		
Solitary Vireo	2	(4)			9	(1)	13	(5)	9	(4)						
Red-eyed Vireo*	9	(1)	8	(4)	5	(1)	6	(2)	26	(4)	21	(2)	11	(3)		
Black-and-White Warbler*	5	(1)	11	(5)			2	(1)			42	(2)	38	(5)		
Tennessee Warbler	4	(4)	4	(1)	21	(2)	26	(6)	54	(4)	46	(1)				
Nashville Warbler	12	(5)	21	(5)			6	(4)	4	(3)	55	(2)	64	(5)		
Magnolia Warbler	33	(5)	57	(5)	53	(2)	27	(8)	21	(4)	56	(2)	25	(4)		
Cape May Warbler*	6	(1)	1	(1)			20	(3)	50	(4)						
Myrtle Warbler	9	(5)	33	(4)	12	(2)	16	(8)	44	(4)	21	(2)	12	(1)		
Black-throated Green Warbler	18	(5)	6	(2)	39	(2)	23	(7)	26	(4)	43	(1)	9	(3)		
Blackburnian Warbler	10	(4)	7	(4)	6	(1)	27	(7)	47	(4)	11	(2)	6	(3)		
Chestnut-sided Warbler*			24	(5)									41	(5)		
Bay-breasted Warbler	47	(4)	9	(2)	28	(2)	102	(8)	158	(4)	45	(1)				
Ovenbird*	37	(2)	25	(4)	3	(1)	56	(4)	20	(4)	85	(2)	54	(5)		
American Redstart	8	(4)	7	(2)	3	(1)	5	(5)			11	(2)	2	(1)		
Rose-breasted Grosbeak*	5	(1)	+	(2)	1	(1)	7	(4)			+	(1)	9	(2)		
Purple Finch*	20	(2)	12	(5)	+	(1)	18	(4)	5	(1)	11	(2)	6	(3)		
Northern Junco	19	(5)	7	(2)			22	(8)	5	(3)	5	(1)	6	(1)		
Chipping Sparrow*			1	(1)	13	(2)	1	(1)					21	(5)		
White-throated Sparrow	24	(5)	61	(5)	15	(2)	27	(8)	24	(4)	67	(2)	64	(5)		
Overall mean density (range)	415 (241–588)		442 (282–615)		317 (277–357)		514 (422–785)		626 (454–831)		914 (667–1158)		533 (377–655)			
Reference numbers (to Appendix 1)	I: 21, 69, 72; IV: Gage		I: 65; 115; II: 120, 128, 154		III: 168, 173		I: 72; II: 154; III: 163; IV: Gage		I: 57, 94		I: 69; III: 218		I: 65; III: 161			

* Data for species marked "*" were not available for some N.B. plots.

Table 6
Summary of data from bird censuses in conifers other than spruce and fir (hemlock, pines, and tamarack). Legend as in Table 3.

Species (birds)	Trees and areas									
	Hemlock N.S.–Ont. (6)		White, Red, Pitch pines Ont. (4)		Jack pine N.B.–Man. (8) [4]		Jack, Lodgepole pines [1] N.W.T.–B.C. (2)		Tamarack Ont.–Man. (8)	
(Spruce or) Ruffed Grouse	1	(1)	6	(2)	(+)	(2)	(+)	(1)	4	(4)
Common Flicker	2	(2)	1	(2)	+	(1)	(+)	(1)	1	(1)
Yellow-bellied Flycatcher					1	(2)				
Least Flycatcher	6	(1)							6	(3)
(Canada or) Blue Jay	8	(3)	15	(3)			(3)	(2)	(+) 2	(3)
(Boreal or) Black-capped Chickadee	19	(5)	23	(4)	+(1)	(3)			6	(3)
Red-breasted Nuthatch	15	(4)	22	(4)	+	(1)			+	(1)
Brown Creeper	12	(6)	+	(1)	+	(1)			1	(1)
Winter Wren	14	(5)							2	(3)
American Robin	4	(1)	12	(1)	2	(4)	11	(2)	3	(3)
Hermit Thrush	19	(4)	+	(1)	15	(8)	1	(1)	+	(2)
Swainson's Thrush	10	(3)			3	(4)	29	(2)	+	(1)
Veery	22	(3)	3	(1)					7	(3)
Golden-crowned Kinglet	7	(3)			1	(3)			2	(2)
Ruby-crowned Kinglet	2	(2)			7	(7)	2	(1)		
Solitary Vireo	10	(3)			2	(5)	+	(1)		
Red-eyed Vireo	22	(5)	18	(3)	1	(2)			19	(2)
Black-and-White Warbler	8	(4)	22	(2)					9	(5)
Tennessee Warbler					7	(4)	15	(1)	22	(5)
Nashville Warbler	12	(4)			4	(5)			62	(8)
Parula Warbler	11	(4)								
Magnolia Warbler	14	(3)			2	(3)			5	(4)
Black-throated Blue Warbler	17	(4)	+	(1)						
Myrtle and/or Audubon's Warbler	10	(2)	2	(1)	15	(8)	46	(2)	14	(5)
Black-throated Green Warbler	67	(6)	37	(2)	1	(2)			+	(1)
Blackburnian Warbler	118	(6)	35	(4)					4	(4)
Bay-breasted Warbler	9	(2)			2	(4)			+	(1)
Pine Warbler			38	(3)						
Ovenbird	74	(6)	62	(4)	2	(2)			+	(3)
Connecticut Warbler					1	(1)			5	(3)
Common Yellowthroat					2	(4)			20	(6)
Purple Finch	6	(3)	12	(3)	2	(2)			3	(2)
Northern Junco	12	(5)	2	(1)	31	(8)	29	(2)	4	(5)
Chipping Sparrow	1	(1)	61	(3)	5	(4)	37	(1)	8	(5)
White-throated Sparrow	31	(4)	+	(1)	14	(7)			35	(7)
Overall mean density (range)	627 (510–878)		625 (435–712)		128 (84–188)		186 (80–292)		320 (236–469)	
Reference numbers (to Appendix 1)	I: 65; II: 134, 154; III: 162, 196		I: 65, 75, 76; III: 228		I: 23; II: 119, 127; III: 167, 200		II: 8; III: 225		I: 25, 47; III: 159, 161	

Plate 3
Jack pine often forms pure stands on dry sandy soils in the boreal region, as well as making up the pioneer forest after fire in many situations. Note the lack of regeneration except in openings, the open canopy, and sparse ground cover — a) sand "blow-out" in opening (Ontario); b) mature lodgepole pine stand (British Columbia); c) dense young stand (Ontario), d) young stand (Quebec).

Plate 3

a

b

c

d

many were also heterogeneous, with considerable areas of northern hardwoods intermingled, which probably contributed to the high densities found.

Stands of white, red, or pitch pines studied in Ontario showed a much less diverse bird fauna with few of the species characteristic of the northern conifer forest (Table 6). One distinctive species, Pine Warbler, was added, and this was the only conifer habitat in which the Brown-headed Cowbird was regularly found. The most regularly common birds:

Black-capped Chickadee, Red-breasted Nuthatch, Blackburnian Warbler, and Ovenbird;

were all shared with the hemlock stands which occupied the same general regions, but others such as:

Blue Jay, Red-eyed Vireo, Black-and-White Warbler, and Ovenbird;

suggest a closer similarity to the deciduous forest. Chipping Sparrow seemed to fill the niche occupied by Northern Juncos in more boreal habitats. Bird densities in these pine stands were little lower than those reported in hemlock, but the plots studied averaged even smaller than for hemlock, as pure pine stands — aside from plantations — were largely confined to thin soils along ridges or to sandy areas.

We also have data from a number of mixed but largely coniferous stands in this region (Table 5). As would be expected, these show a larger number of regular species. In particular, Chestnut-sided and Canada Warblers occurred more often here than in either strictly conifer or strictly broad-leafed plots. Greater or less proportions of conifer and deciduous trees on individual plots could often be recognized by the relative representations of the appropriate bird communities, but generally the habitat data for these plots were too poor for useful conclusions. Total densities were also high, in the range from 450 to 800 pairs per km², which is encouraging inasmuch as heterogeneous stands make up major proportions of most forests in settled areas of Canada.

1.4. Jack pine

In the main boreal forest, the only pine is jack pine, which is most often found on xeric sites such as eskers, old dune areas, and rocky outcroppings, as well as in early succession after fire. No bird species is restricted to this community, which is clearly an impoverished variant of the typical spruce forest fauna. Species found in most jack pine stands (Table 6) included:

Hermit Thrush, Ruby-crowned Kinglet, Myrtle Warbler, Slate-coloured Junco, and White-throated Sparrow;

with other frequent species such as:

American Robin, Swainson's Thrush, Solitary Vireo, Tennessee Warbler, Nashville Warbler, Chipping Sparrow.

Jack pine stands are much more open than spruce or fir or hemlock forests, commonly averaging only 20 to 30% canopy cover, and some differences from the closed stands probably reflect this, in particular the dominance of Hermit Thrush over Swainson's Thrush.

Overall, densities of birds in jack pine are very low for a forest habitat, usually in the range from 80 to 200 pairs per km², which is less than in many field or prairie samples where a tree layer is totally lacking. However, these xeric sites with pine canopy usually lack a shrub layer entirely, and thus include only canopy species and ground-nesting birds.

1.5. Bog forest

The last needle-leafed forest type of the boreal biome is the bog forest dominated by tamarack, alone or with low black spruce, which in turn grades off into more open bogs (to be discussed in a later section). As already noted under succession, these are often present only as marginal zones around a depression or along a swale, and are usually difficult to work in, as well as being small in area, so are little studied. The birds most often detected in the tamarack and bog forest samples are a peculiar mixture of species more usually considered typical of other types of habitat (Table 6) including:

Cedar Waxwing, Red-eyed Vireo, Tennessee, Nashville, and Myrtle Warblers, Common Yellowthroat, Slate-coloured Junco, and Chipping and White-throated Sparrows.

Notable among these is the absence of any thrush (the ground being possibly too wet), the relative dominance of Nashville Warbler, and the presence of Cedar Waxwing and Common Yellowthroat, which are characteristic of edges and of low shrubbery respectively. The presence of Tennessee Warblers too is probably correlated with the alder understorey often associated with such damp areas, rather than with the tamaracks. Most other species, including those found less regularly, are characteristic of other northern conifer forests. Total bird densities found in these habitats, in the range of 200 to 450 pairs per km², are comparable to those in spruce stands in similar regions, although the small size and heterogeneity of the tamarack plots may have exaggerated their densities.

1.6. Rockies to coast range

To round out the picture of northern conifer forests, one must discuss separately such forests occurring in British Columbia between the Rocky Mountains and the coast range. These exhibit obvious differences but also pronounced similarity or parallelism in their common bird species, compared with more eastern areas. Probably the most evident difference, as one approaches and passes the Rockies, is the disappearance of a large proportion of the typical boreal forest warblers; no other family shows a comparable diminution here and none shows an equivalent increase in numbers of species (Snyder 1950). A number of species are replaced by western sibling species or subspecies, notably Tennessee by Orange-crowned Warbler, Myrtle by Audubon's Warbler, Black-throated Green by Townsend's Warbler, Mourning by MacGillivray's Warbler, and Slate-coloured by Oregon Junco.

As already noted, a wide variety of needle-leafed forests occur in the varying

Plate 4
The subalpine forest of British Columbia is a mixed type including subalpine fir, Englemann spruce, and lodgepole pine, but its bird fauna as well as its general appearance suggest a close parallel with the spruce stands of the main boreal region. Note the characteristic "steeple" growth form, perhaps an adaptation to heavy snowfalls.

Plate 5
Immediately south of the boreal region in British Columbia is a more open, dry forest characterized by Douglas fir. Note the virtual absence of ground cover — this site, on an island, has never been grazed.

Plate 4

Plate 5

topographic and altitudinal situations of British Columbia's mountains, plateaux, and valleys, and the birdlife also varies greatly. However, despite differences in numbers, the quality of birdlife is very similar, without great variation in the presence or absence of many species, particularly north of latitude 53°N. The common and widely distributed birds of the (largely) spruce forests of central British Columbia (Table 3) include:

Hammond's Flycatcher, Canada Jay, Black-capped Chickadee, Red-breasted Nuthatch, Winter Wren, American Robin, Swainson's Thrush, Golden-crowned Kinglet, Ruby-crowned Kinglet, Audubon's Warbler, Western Tanager, Pine Siskin, Oregon Junco;

thus showing a marked parallel in composition to the community in spruce stands east of the Rockies, aside from the scarcity of warblers. Most of these species ranged from valley bottom to near timberline in these latitudes (53–56°N), but Hammond's Flycatcher was lacking from all the subalpine forest stands reported. In this higher zone, subalpine fir forms an important part of the canopy, and here Townsend's and Blackpoll Warblers are present as well as the species listed above, while Mountain Chickadees replace Black-capped Chickadees. The virtual absence of Boreal Chickadees in central British Columbia forests is a surprise, in view of their regularity in spruce and fir stands east of the Rockies, and that of Chestnut-backed Chickadees on the west coast. (Smith 1967, Sturman 1968). The lack of any common emberizid sparrows other than Oregon Juncos on forest plots is also notable, as members of this group were common and well-distributed on roadside counts in this region. A number of common species noted in these samples were associated with intrusions of broad-leafed trees and shrubs in the study areas, and these are discussed later under that heading. Densities in these habitats ranged from 130 up to over 500 pairs per km^2, the lower figures being from the subalpine zone.

1.7. Other western forests south of the boreal region

We have no quantitative data for the drier, more open conifer forests of the interior Douglas fir zone (Tisdale and McLean 1957) and the ponderosa pine zone, nor for the humid Columbia Forest Region of southeastern British Columbia. The bird community of the largely coniferous Coast Forest of British Columbia has recently been described by Buckner *et al.* (1975). It shares some species with the central interior of the province, but fewer with regions east of the Rockies. Major species include:

Western Flycatcher, Chestnut-backed Chickadee, Winter Wren, American Robin, Varied Thrush, Swainson's Thrush, Golden-crowned Kinglet, Townsend's Warbler, and Oregon Junco.

Densities, in the range of 200 to 500 pairs per km² (higher in successional habitats), are comparable to those found for interior spruce forests.

Similarities and differences of the bird fauna of the western boreal region of Canada in comparison with those of the conifer forests further south may now be considered briefly. Census data for the western coniferous forests of the United States are sketchy. Ideally, one should restrict such comparisons to the subalpine forests of Englemann spruce and subalpine fir and lodgepole pine, ignoring both the frost-hardy timberline stands and the more drought-tolerant forests at lower levels. Most census data, however, are from mixed conifer stands, including Douglas fir and even ponderosa pine from the lower montane forest, which is much more open than the subalpine and boreal forest types. Many common birds are widespread through all the western conifer habitats, as shown in Table 7. What this table does not show is that the more open and topographically varied forests of southern interior British Columbia and adjacent states also contain a variety of birds more properly associated with deciduous shrub-

Table 7
Composition and density of breeding bird communities of western coniferous forests of Canada and adjacent United States.

	Mean density (males/km²) in conifer stands					
Species	NE. B.C., S. Mack. (5)* 58–61° N†	Cen. int. B.C. (4) 54–56° N†	S. int. B.C., Ida., W. Mont. (5) 46–50° N‡	Coastal B.C. (5) 48–55° N§	Utah, Wy., E. Ore., E. Calif. (5) 39–45° N‖	Colo. (9) 38–41° N#
Spruce Grouse	7 (2)	+ (1)	2 (1)			
Hammond's Flycatcher		11 (2)	23 (4)			
Canada Jay	6 (4)	4 (4)				1 (1)
Steller's Jay				10 (4)	3 (2)	1 (3)
Boreal Chickadee	10 (5)					
Mountain Chickadee		1 (1)	10 (4)		55 (5)	20 (8)
Chestnut-backed Chickadee			28 (5)			
Red-breasted Nuthatch	2 (1)	8 (3)	7 (3)	4 (4)	25 (3)	1 (3)
Brown Creeper		3 (1)	+ (1)	9 (3)	17 (3)	3 (3)
Winter Wren		8 (3)	7 (2)	55 (5)		
American Robin	2 (1)	12 (3)	5 (2)	54 (5)	30 (5)	10 (8)
Varied Thrush	1 (1)	6 (2)	5 (2)	28 (5)		
Swainson's Thrush	39 (5)	38 (4)	48 (5)	35 (5)		
Golden-crowned Kinglet	5 (2)	46 (4)	22 (3)	30 (5)	30 (4)	
Ruby-crowned Kinglet	28 (5)	36 (4)	15 (2)		72 (5)	15 (4)
Solitary Vireo	7 (1)	4 (1)	7 (3)			5 (4)
Tennessee Warbler	30 (4)	12 (2)				
Orange-crowned Warbler				11 (4)		
Yellow-rumped Warbler	55 (5)	12 (3)	30 (5)	15 (3)	32 (5)	23 (8)
Townsend's Warbler		20 (2)	10 (1)	22 (4)		
MacGillivray's Warbler		12 (2)	27 (3)	19 (4)		
Wilson's Warbler		12 (2)		17 (5)	1 (1)	
Western Tanager	10 (2)	8 (3)	23 (5)	19 (4)	40 (3)	10 (4)
Pine Siskin		12 (4)	20 (4)	2 (1)	41 (4)	23 (8)
Northern Junco	39 (4)	27 (4)	54 (5)	14 (3)	30 (4)	
Gray-headed Junco						23 (8)
Chipping Sparrow	49 (5)	3 (3)	54 (4)		70 (3)	7 (4)
White-throated Sparrow	2 (1)	2 (1)				
Mean density (/100 ha) of all species	316	469	500	608	726	220
Mean density of above species (% of total)	292 (92)	297 (63)	369 (74)	372 (61)¶	496 (68)	131 (59)

* Number of plots included.
† Data from Table 3.
‡ Data from Aud. Field Notes (Grant 1965, Longley 1944, Manuwal 1967 (2 plots)), and Amer. Birds (Frissell 1973).
§ Data from Buckner *et al.* (1975), mature plots only.
‖ Data from Aud. Field Notes (Burr, 1969 [2 plots], Robert 1966, Webster 1967), and Amer. Birds (Archie 1973).
Data from Aud. Field Notes (Hering 1956, 1958; Thatcher 1955 [2 plots], 1956), and Condor (Hering 1948, Snyder 1950 [3 plots]).
¶ Including replacement series.

bery and edge (e.g., Black-billed Magpie, House Wren, Townsend's Solitaire, and Rufous-sided Towhee) or with the ponderosa pine zone (e.g., White-breasted and Pigmy Nuthatches, Western Bluebird, and Cassin's Finch). Very few of these birds extend northward into the boreal forest of central British Columbia, the exceptions including Dusky Flycatcher, Western Wood Pewee, and Orange-crowned, MacGillivray's, and Wilson's Warblers. There is no clear-cut southern limit to the boreal region west of the Rocky Mountains, but the Kitimat–Banff line roughly approximates the limits both of the "dry belt" vegetation and of the southwestern avifauna that accompanies it.

The forest types discussed in these paragraphs were excluded from the boreal region (see The northern forest biome: 1. Environment), but brief consideration of their bird communities here should help one to understand the relationships of the northern British Columbia communities with those of the main boreal forest.

1.8. Other eastern forests south of the boreal region

In the eastern United States, conifer forests other than hemlock and various pines (considered above), but excluding the southeastern pinelands, are restricted in extent. The forests of northern Maine are here considered as boreal (Fig. 1; Stewart and Aldrich 1952). The Appalachian Mountains at higher elevations are characterized by a red spruce–Fraser's fir forest superficially comparable to the boreal conifer climax. All of the major bird species of these forests are found also in the boreal forest, at least in its southeastern portions. However, a number of characteristic boreal species drop out as one moves south through the mountains, particularly Canada Jay, Boreal Chickadee, Ruby-crowned Kinglet, and the budworm-following warblers. Yellow-bellied Flycatcher and White-throated Sparrow extend farther south, but by West Virginia and North Carolina the bird community — as already noted by Stewart and Aldrich (1952) — is more like that found farther north in the hemlock-or white pine-dominated stands than that of typical boreal forest. Census data from the eastern mountains are scanty, but they agree reasonably well with each other. The few census data from conifer habitats of northern Michigan and Minnesota show very little of a boreal nature, and breeding bird survey data from adjacent parts of Ontario confirm that this area is transitional rather than boreal.

1.9. Cardueline Finches

The cardueline finches deserve special mention in the picture of boreal conifer birds. Most of these species extend coast to coast in the boreal region, but owing to their largely non-territorial behaviour they are seldom reported as breeding birds on (mapping) census plots, though sometimes classed as visitors. These are members of a group of birds specialized to feed on seeds of various trees (Newton 1972). As some tree species set seed only in alternate years or at longer intervals in a given area, the presence of cardueline finches is less predictable than that of most other birds, and some are totally absent in one year from areas where they were abundant in another (Bock and Lepthien 1976). None of the six common species associated with conifer forests during the breeding season — Evening Grosbeak, Purple Finch, Pine Grosbeak, Pine Siskin, and Red and White-winged Crossbills — feeds exclusively on conifer seeds, though all do so to some extent. Purple Finch has already been noted as characteristic of fir stands, but it is widespread in other conifer forests, if seldom regular or abundant on census plots there.

Particular note may be made of the correlation of occurrence in summer of Evening Grosbeaks, and to a lesser extent Purple Finches, with areas of spruce budworm concentrations. For example, in budworm epidemic areas in central New Brunswick, flocks totalling 500 or more Evening Grosbeaks might be seen in a drive of 2 or 3 hours through conifer and mixed forests. In 1968-69 I frequently noted from 60 to 100 individuals calling on or over a census plot in the course of one survey lasting 3 or 4 hours there, without being able to conclude that they were actually breeding on the plot. Evening Grosbeaks, with Tennessee Warblers, are one of the best biological indicators of the presence of spruce budworm, short of sampling the caterpillars themselves, as they start to build up before damage to trees is at all obvious, and are so conspicuous as to be easily detectable from a passing vehicle. The main budworm areas at present include New Brunswick and central Quebec, with parts of Ontario and British Columbia, and the co-operative Breeding Bird Survey shows that Evening Grosbeaks and Tennessee Warblers are most frequent and in highest relative numbers there.

In the absence of useful quantitative data on these species from census plots, my notes and impressions with published qualitative data must suffice. In summer, I associate Evening Grosbeaks, Pine Siskins, and White-winged Crossbills especially with spruces, although Siskins are also common in many other situations. Red Crossbills, too, were common in spruces in Newfoundland and Cape Breton Island in 1968, but I have seldom found them elsewhere except in the Douglas fir zone of British Columbia; published sources agree that this species is regular throughout the conifer forests of western North America. My observations of Pine Grosbeaks show no clear association of this species with any particular boreal forest type and the literature, including Newton's (1972) monograph of the finches, agrees that they frequent a wide variety of wooded areas, although most nests in North America have been in conifers.

1.10. Young conifer stands

There seem to be no Canadian studies of birds of the young conifer stands early in upland succession. This in part is

Plate 6
White spruce takes over abandoned fields in the Maritime Provinces, which happens without an intervening pioneer tree species if a seed source is available — this example is on Cape Breton Island, N.S.

Plate 6

owing to the frequent early appearance of broad-leafed species such as poplars, willows, alder, or fire cherry, in whose shade the first conifers develop (Hagar 1960, Conner and Adkisson 1975 on succession after clear-cutting in the USA). However, even censuses of old fields grown up with white spruce, or of young stands of spruce or fir, are lacking in Canada. We are left with such inferences as may be drawn from the inclusion of patches of young conifers in the older stands studied, but omitting areas with growth so young or so open that birds characteristic of open or low shrubby areas formed a major part of the community. No species is unique to young conifer stands, although in the east Blackpoll Warblers and Lincoln's Sparrows are largely found in young, or at least low, spruces. Other species more common in young than in mature conifer stands are more widespread, including:

> Yellow-bellied Flycatcher, American Robin, Hermit Thrush, Magnolia Warbler, Slate-coloured Junco, and White-throated Sparrow;

whereas many species characteristic of mature conifer stands are scarcer or lacking, for example:

> Canada Jay, Red-breasted Nuthatch, Brown Creeper, Swainson's Thrush; Black-throated Green, Blackburnian, and Bay-breasted Warblers; and Purple Finch.

The common birds of young stands thus include American Robin and White-throated Sparrow, which are probably the most obvious as well as among the most common birds associated with wooded habitats, and especially forest edges, in all the boreal and near-boreal regions of Canada, except for the scarcity of Whitethroats west of the Rockies. The need for systematic data on birds of successional and edge habitats could hardly be made more obvious.

1.11. Other species

To complete the discussion of birds of the needle-leafed forest, I mention here a number of wide-ranging species not mentioned under any community or successional stage. These are not confined to one community or even to one forest type, and thus are difficult or impossible to classify precisely. They include particularly the raptorial birds, among which Goshawk, Red-tailed Hawk, some races of Merlin, Great Gray Owl, Hawk Owl, Boreal Owl, and Common Raven may be considered more characteristic of conifer than of broad-leafed forests, though by no means restricted to them. The Black-backed Three-toed Woodpecker is also characteristic of spruce or fir forests, but was not found regularly in any region. As it was more often noted in Algonquin Park and in New Brunswick than elsewhere, it may be more characteristic of the transitional zone than of the main boreal forest (Short 1974).

2. Broad-leafed forests

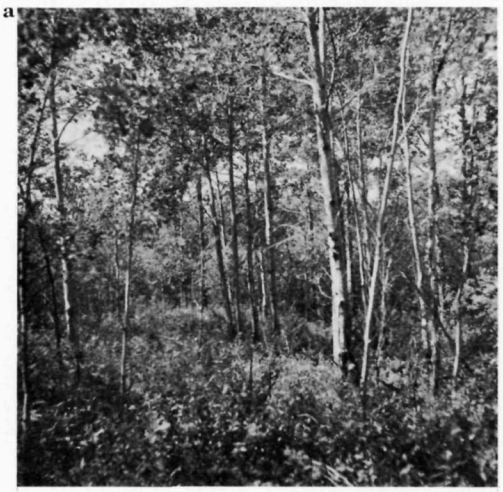
Bird census work in North America, as in Europe, really began in broad-leafed forests. The temperate deciduous forest biome of eastern North America includes those areas both longest and most densely settled of any on this continent, and it is also relatively easy to work in. Williams' (1936) study is usually taken as the pioneering effort here, although various European workers were following parallel courses at the same period. Later work by Kendeigh and his associates and by Odum and Johnston in more southern areas has given a good picture of the bird community both in the southern oak and hickory types and in the northern beech and maple forests (Webster and Adams 1973). All these forest types drop out before the main boreal forest, though the last-named has a place in the transition zone of southern Canada and the northern states. Until the past decade, very little work was done on the birds of poplar and birch stands within the boreal region. Flack (1976) has recently discussed birds of aspen stands in western North America, including the parklands of Canada's Prairie Provinces.

Kendeigh (1948) termed the bird community of climax northern hardwood

Plate 7
Poplars are strictly successional in nature, and are typically succeeded by spruce or fir within a century — a) young aspen stand (Alberta); b) mature aspens (note total defoliation by forest tent caterpillar in mid-June) with well-grown spruce succession (Saskatchewan); c) on the fertile floodplains of the far west, black cottonwoods reach immense size (British Columbia); d) balsam poplar readily colonizes river gravels (British Columbia).

Plate 7

a



b

c

d

Plate 8
Trembling aspen, with balsam poplar on damper sites, is probably the most common and widespread pioneer tree in the boreal region. Note particularly the very dense understorey and shrub layers — a) aspen/balsam poplar above alder (Ontario); b) aspen/balsam poplar above mountain maple (Manitoba); c) balsam poplar above ostrich fern (Manitoba); d) aspen/willow (British Columbia).

forest the *Vireo–Seiurus* (Red-eyed Vireo–Ovenbird) biociation. Those species are also dominants in boreal poplar and birch stands in Canada. But Kendeigh's *Spizella–Tyrannus* (Field Sparrow–Eastern Kingbird) deciduous forest-edge biocies has no carry-over to the boreal region where, if such a grouping were to be recognized, it would be defined by very different species such as Alder Flycatcher and Chestnut-sided Warbler. Poplar and birch habitats show less variation than either needle-leafed forests or more southern hardwood stands, since they do not reproduce in their own shade, and thus form only transient stands which are usually succeeded by conifers within a few decades, except in parts of western North America (Flack 1976). Furthermore, boreal broad-leafed stands develop only on a relatively narrow range of soil and moisture types, since jack pine is the pioneer tree on dry and sandy sites, and black spruce, tamarack, or alder on various wet and peaty to mucky sites. Thus, boreal broad-leafed forest is restricted both in duration on a site and in site variety, so its lack of a unique avifauna is less surprising.

Only three tree species dominate the boreal broad-leafed forests of North America, trembling aspen being much the most important and widespread. Balsam poplar, which occurs alone on river gravels, also mixes with aspens on damp sites. Paper birch often occurs with aspen on dry sites but seldom is dominant, although individual birch trees may persist long after the aspens have been succeeded by conifers. Beaked willow and speckled alder seldom reach into the canopy, although they often form a dense understorey on damp sites. Other small trees such as mountain maple, fire cherry, and water birch, are important only in the understorey, beneath openings in the canopy, or in early successional stages. I have detected no consistent differences between the bird communities of broad-leafed stands dominated by the different canopy species of trees, but the type and extent of the understorey may greatly influence the birds encountered.

Plate 8


a


b


c

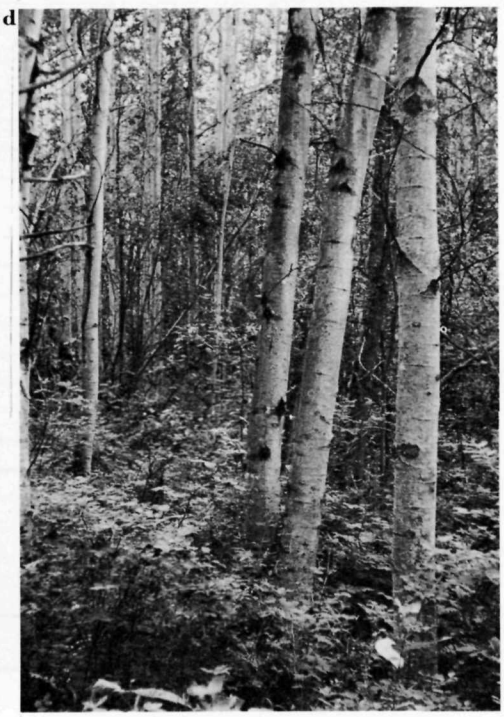

d

Table 8
Summary of data from bird censuses in stands dominated by poplars or birches.
Legend as in Table 3

Species	Area									
	N.B., Que., S Ont. (Algon. Pk.)		Cen. Ont. (clay belt)		Man.–Sask.		NE B.C. (Alaska Hwy)		Cen. B.C. (Smithers)	
	(5)	[1]	(1)	[1]	(4)	[3]	(3)	[2]	(2)	[2]
Ruffed Grouse	4	(2)	5	(1)	+	(1)	4	(2)	3	(2)
Yellow-bellied Sapsucker	4	(2)	1	(1)			8	(3)	1	(1)
Downy Woodpecker			1	(1)	1	(1)			2	(1)
Least Flycatcher	40	(4)	81	(1)	17	(3)	8	(3)	24	(1)
Dusky Flycatcher									32	(2)
Black-capped Chickadee	15	(4)	3	(1)	2	(2)	2	(1)	9	(2)
American Robin	12	(4)	15	(1)	3	(1)	7	(3)	19	(2)
Hermit Thrush	24	(4)	1	(1)	1	(1)				
Swainson's Thrush	4	(1)	20	(1)	6	(2)	20	(3)	53	(2)
Veery	39	(4)	9	(1)	11	(1)				
Red-eyed Vireo	55	(5)	25	(1)	76	(4)	17	(3)	2	(1)
Philadelphia Vireo			57	(1)	7	(2)				
Warbling Vireo									99	(2)
Black-and-White Warbler	6	(4)	6	(1)	14	(3)	3	(1)		
Tennessee Warbler					26	(3)	3	(3)		
Orange-crowned Warbler					1	(1)			11	(2)
Nashville Warbler	4	(2)	1	(1)						
Magnolia Warbler	10	(4)	1	(1)	1	(1)	18	(3)		
Black-throated Blue Warbler	19	(3)	1	(1)						
Yellow-rumped Warbler	3	(2)			1	(1)	5	(1)	16	(2)
Black-throated Green Warbler	1	(1)			9	(1)	5	(1)		
Chestnut-sided Warbler	11	(3)	7	(1)	7	(2)				
Ovenbird	106	(5)	56	(1)	66	(4)	32	(3)		
Mourning Warbler	+	(1)	25	(1)			+	(1)		
MacGillivray's Warbler									18	(2)
Canada Warbler	15	(3)			3	(1)	3	(1)		
American Redstart	24	(5)	5	(1)	66	(2)	12	(2)	150	(2)
Brown-headed Cowbird	5	(1)			6	(1)	3	(1)	14	(2)
Rose-breasted Grosbeak	8	(4)			4	(2)	5	(3)		
Purple Finch	2	(4)							7	(1)
Northern Junco	17	(5)					10	(2)	4	(2)
Chipping Sparrow					18	(2)	12	(2)		
White-throated Sparrow	18	(4)	18	(1)			1	(2)		
Overall mean density (range)	479 (337–672)		347 (—)		371 (224–520)		223 (156–301)		578 (471–686)	
Reference numbers (to Appendix 1)	I: 20, 65, 69; III: 163		II: 118, 125		III: 161, 165, 171, 172		III: 176, 177, 190		III: 221, 222	

2.1. Dominant bird species

Bird species typical of poplar or birch stands in the boreal region include (Table 8):

Ruffed Grouse, Yellow-bellied Sapsucker, Least Flycatcher, Black-capped Chickadee, American Robin, Swainson's Thrush (W from 80°W), Veery (E from 105°W), Red-eyed Vireo, Black-and-White Warbler, Ovenbird, Canada Warbler, American Redstart, and Rose-breasted Grosbeak.

Some of these respond particularly to certain vegetational combinations in the forest; for example, Least Flycatchers are usually associated strictly with aspens, avoiding balsam poplar or birch, probably owing to the more open situation immediately below an aspen canopy (Breckenridge 1956). American Redstart may be a dominant species where a dense subcanopy, at a height of 3 to 9 m (10–30 ft), is present below the main poplar canopy, but elsewhere it may be scarce or even lacking. Several other species frequently reported from broad-leafed stands are actually associated with scattered trees or clumps of trees of needle-leafed species, especially white spruces or balsam firs, within the hardwood stand. The most frequent birds in this category are:

Hermit Thrush, Magnolia Warbler, Slate-coloured Junco, and White-throated Sparrow.

All of these tend to be associated with a rather open canopy or rather small trees. Least Flycatchers, on the other hand, clearly avoid areas with conifers in the canopy or subcanopy. Another group of species is associated with openings, or young growth or understorey of similar height, but of broad-leafed trees rather than of conifers. This includes:

Philadelphia Vireo; Tennessee, Nashville, Chestnut-sided, and Mourning Warblers; and Chipping Sparrow (W from 100°W).

Of these, Philadelphia Vireo and Mourning Warbler will occupy tall deciduous shrubbery under a dense poplar canopy as well as in openings, whereas the others occupy such shrubbery only in the absence of or in openings in the canopy. Nashville and Tennessee Warblers seem to be eastern and western counterparts in this context, as no broad-leafed plot showed both species.

Many other species seem more characteristic of the transitional maple and beech forests in eastern Canada, though sometimes extending far into the boreal region in broad-leafed or mixed habitats. Among these are:

Hairy and Downy Woodpeckers, Eastern Wood Pewee, Blue Jay, White-breasted Nuthatch, Parula and Black-throated Blue Warblers, and Scarlet Tanager.

Even among the regular and dominant birds, a number attain higher densities in maple and other northern hardwood stands than in poplars or birches, perhaps reflecting increased productivity with the longer growing seasons in more southern areas.

Overall, densities reported for boreal poplar and birch stands range from 200 to over 600 pairs per km^2, the lower figures being either from younger stands or towards the northwest beyond Manitoba, where the influence of the eastern hardwood forest rapidly falls off. Stands from Ontario eastward show a range of densities similar to or slightly lower than those from the most northerly maple stands in eastern Canada, which show from 400 to 650 pairs per km^2.

2.2. West of the Rockies

Birds of broad-leafed stands west of the Rockies are more distinct from those of the eastern boreal forest than are those of needle-leafed forests in the west, because most of the dominant warblers do not range west of the mountains. Our data for these habitats in British Columbia are even sketchier than for coniferous forest. There are few common and regular species of birds, and most are associated with small trees or tall shrubbery rather than with high forest. They include:

Least Flycatcher (S to 51°N), Dusky Flycatcher, Western Wood Pewee, Black-capped Chickadee, American Robin, Swainson's Thrush, Red-eyed Vireo (N to 55°N), Warbling Vireo, Orange-crowned and MacGillivray's Warblers, and American Redstart.

In central British Columbia, it was striking to find that Warbling Vireos were the most common vireo even with the elsewhere dominant Red-eyed Vireo present. However, the latter did not arrive until mid-June, three weeks or more after the Warbling Vireos, both at 100 Mile House in 1958–59 and at Smithers in 1975. Here too, north of 53°N, the American Redstart was by far the most common warbler in all broad-leafed woodlands, though here as in the east it favoured the subcanopy or sapling layers rather than the high canopy. MacGillivray's Warbler, like the closely related Mourning Warbler, occurred in tall shrubbery whether this was under a canopy or in the open. Largely owing to the very high density of American Redstarts, the total bird densities found on study areas in these habitats were in the range from 400 to over 600 pairs per km^2, as high as in the east.

Most of the species characteristic of broad-leafed habitats in British Columbia also occurred where such trees or tall shrubs intruded into largely needle-leafed study areas, none showing an obvious lower limit to the acceptable area of suitable habitat. Such adaptability may be related to the apparent expansion by certain birds in British Columbia to fill several niches which are occupied by different species in the main boreal forest. For example, in central British Columbia the Swainson's Thrush, in addition to its typical spruce–fir habitat, occupies the open pine forests where Hermit Thrushes would be expected east of the Rockies, and also occupies the broad-leafed stands where Veeries are characteristic from Manitoba eastwards. Veeries were lacking this far north, and the few Hermit Thrushes were too scattered to give any impression of a characteristic niche. Niche expansion was also obvious from the work of Theberge (1976) in southwestern Yukon

Plate 9
Swainson's Thrush, though primarily a bird of the spruce and fir forests in eastern Canada, occupies also the successional poplar stands west of the range of its congener, the Veery — this nest in poplar forest was in Alberta.

Plate 9

Territory, where he found the same three species, Swainson's Thrush, Myrtle Warbler, and Slate-coloured Junco, dominant in all forest types, whether conifer or broad-leafed, successional or climax.

2.3. Some comparisons

Although western North America is noted for its diverse avifauna, this is much more striking in the southwestern USA, where varied habitats and resident populations have led to many more groups of closely related species (e.g., hummingbirds, *Myiarchus* flycatchers, thrashers, *Vermivora* warblers, *Aimophila* sparrows) than in Canada.

The work of Flack (1976), though unfortunately based on methods differing from the standard mapping census used in the present study, provided a welcome review of the situation in areas immediately to the south of the boreal forest in western Canada. Predictably, aspen stands here featured some birds characteristic of broad-leafed stands west of the Rockies, as well as others widespread farther east, and a number which do not penetrate the main boreal region at all. His presentation listed only one stand he considered as boreal, and comparisons with the whole of our data confirm that differences between this and his other Canadian stands are typical of those between the parkland belt and more northern boreal aspen stands. These include particularly the presence or increased abundance to the north and east of Red-eyed Vireo and Ovenbird, and the presence or increased abundance to the south and west of Downy Woodpecker, Western Wood Pewee, House Wren, Veery, Warbling Vireo, and Baltimore Oriole, as well as Yellow Warbler, American Goldfinch and Clay-coloured Sparrow, which in the boreal region are birds of open shrubby areas rather than forest. All this confirms Flack's view that boreal aspen stands have a bird fauna depauperate in comparison with that of the parklands, which are a mixing ground for both eastern and western forest species as well as birds from the prairie edge.

The relationships of the avifauna of eastern boreal broad-leafed stands may be examined by comparison with other census data (Table 9). There is almost a complete overlap between the birds of boreal poplar and birch stands and of the northernmost maple and/or beech stands censused in Canada; much more than between the latter and those of the main beech–maple region (Webster and Adams 1973). The latter included many important birds of the understorey, e.g., Tufted Titmouse, House Wren, Cardinal, Rufous-sided Towhee, not found in the Canadian maple-beech stands. On the other hand, the poplar–birch stands included a large number of species more typical of the mixed and fir-dominated stands of the eastern boreal forest; many of these were also present, but much scarcer, in the Canadian maple–beech stands, and were wholly lacking in the more southern ones. They often reflected the presence of some conifer in most poplar–birch stands, which occur strictly as successional stages.

2.4. Early stages

As previously noted, little census work has been done in Canada in early stages of succession, but data from intrusions of such habitats into more mature forest combined with the few censuses of young broad-leafed stands give relatively unambiguous results. The low shrubby stages have a distinct bird community, whereas stands of young trees 5 m (15 ft) or more in height mainly feature forest birds. Accordingly, the low shrub community will be discussed in part 4. Open habitats (p. 40); only young trees are considered here. These habitats have no unique birds, but include some that persist only in the understorey of more mature stands, while others are tolerant and widespread. The most regular birds of young broad-leafed stands are:

> American Robin, Swainson's Thrush, Red-eyed Vireo, Philadelphia Vireo; Tennessee, Chestnut-sided, and Mourning Warblers; American Redstart, and White-throated Sparrow.

Plate 10
Willows and alders often form almost impenetrable thickets, both in the early stages of forest succession and in damp sites under the canopy of boreal forests — a) willows in old fields (Quebec); b) alders in gully (Quebec).

Plate 10

a

b

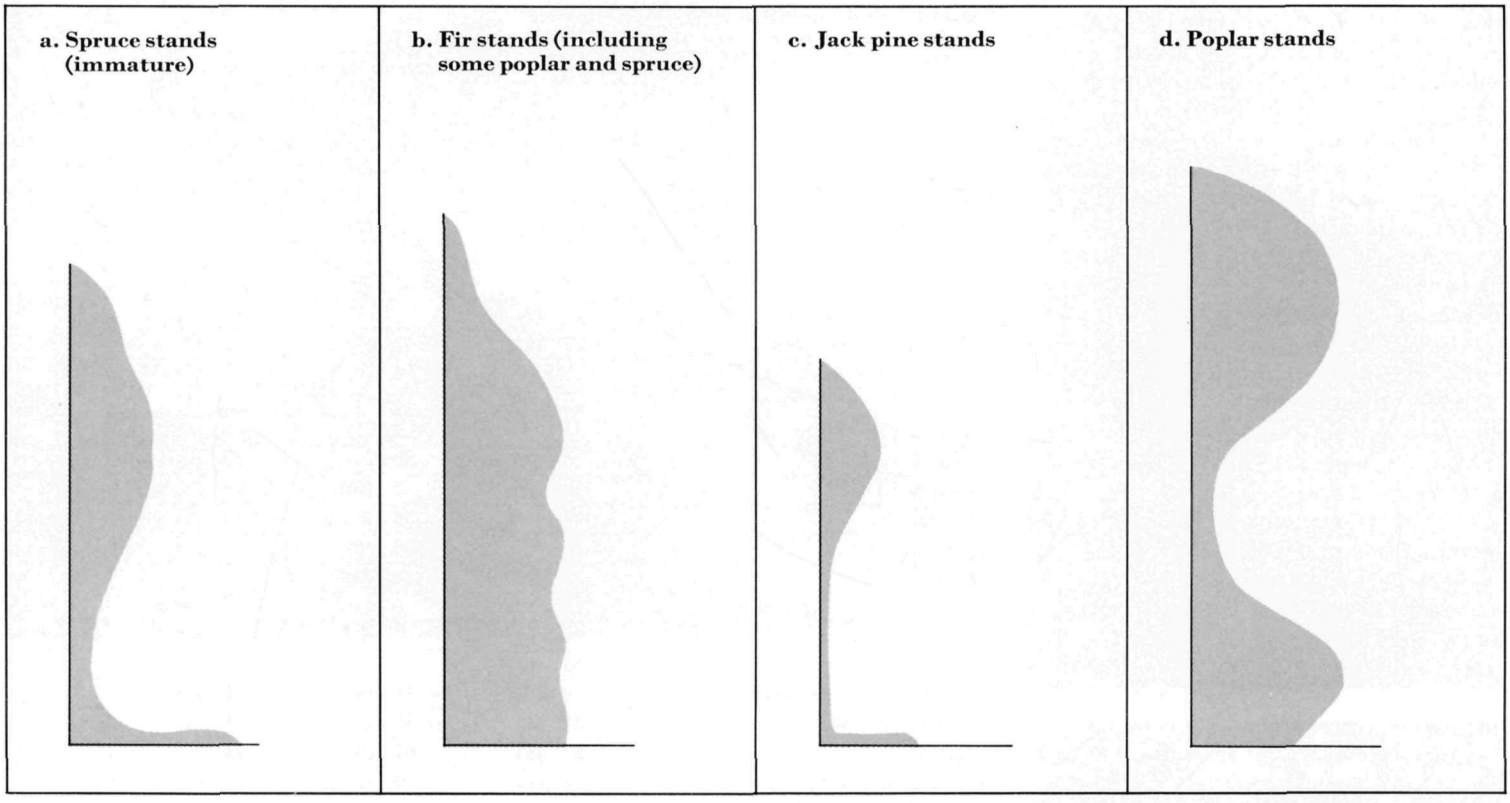
Table 9
Composition and density of breeding birds of Canadian boreal poplar stands compared with those of other communities

	Density, males/km², in stands of			
	*Abies**	*Populus* &/or *Betula*†	*Acer* and/or *Fagus*	
Species	N.B.–Ont. (6) Lat. 46–47°N	N.B.–Ont. (6) 46–48°N	N.S.–Ont. (11)‡ 44–47°N	Ohio–Ind. (9)§ 39–42°N
Ruffed Grouse	8 (5)	4 (3)	1 (4)	1 (3)
Yellow-bellied Sapsucker	6 (4)	3 (3)	11 (10)	—
Downy Woodpecker	—	+ (1)	5 (7)	22 (9)
Least Flycatcher	4 (1)	47 (5)	94 (10)	—
Eastern Wood Peewee	3 (2)	2 (1)	11 (9)	40 (9)
Black-capped Chickadee	9 (4)	13 (5)	2 (5)	20 (7)
White-breasted Nuthatch	—	6 (2)	5 (7)	20 (9)
American Robin	5 (4)	13 (5)	3 (4)	ca. 3 (est.)
Wood Thrush	—	2 (1)	6 (6)	47 (9)
Hermit Thrush	6 (2)	20 (5)	10 (5)	—
Swainson's Thrush	18 (4)	7 (2)	2 (2)	—
Veery	—	34 (5)	29 (9)	1 (1)
Red-eyed Vireo	18 (4)	50 (6)	94 (11)	74 (9)
Philadelphia Vireo	5 (1)	10 (1)	—	—
Black-and-White Warbler	15 (5)	6 (5)	6 (5)	—
Nashville Warbler	18 (6)	3 (3)	1 (2)	—
Magnolia Warbler	63 (6)	8 (5)	2 (1)	—
Black-throated Blue Warbler	9 (3)	16 (4)	33 (10)	—
Chestnut-sided Warbler	22 (4)	10 (4)	1 (3)	—
Ovenbird	37 (5)	97 (6)	71 (11)	42 (6)
Mourning Warbler	4 (2)	4 (2)	1 (2)	—
Canada Warbler	17 (4)	12 (3)	3 (2)	—
American Redstart	16 (4)	21 (6)	36 (7)	27 (5)
Brown-headed Cowbird	3 (1)	4 (1)	+ (1)	10 (9)
Scarlet Tanager	2 (2)	2 (2)	13 (8)	17 (8)
Rose-breasted Grosbeak	2 (3)	7 (4)	14 (9)	ca. 1 (est.)
Northern Junco	14 (4)	14 (5)	2 (5)	—
White-throated Sparrow	55 (6)	18 (5)	1 (1)	—
Mean density of all species	568	457	507	712
Mean density of above species (%)	359 (63)	433 (95)	457 (90)	325 (46)

* Usually mixed with *Picea* and/or *Populus* and/or *Betula;* data from Table 5.
† Data from Table 8.
‡ Data from references in Appendix 1 — I: 65, 69; II: 134, 143, 154; III: 157, 163, 196, 228.
§ Data from Webster and Adams, 1973.

Figure 4
Schematic vegetation profiles for major forest habitats studied in the boreal region. Relative tree heights, percent canopy cover, and percent ground cover based on data in Appendix 2

Figure 4



Both Mourning Warbler and White-throated Sparrow of Kendeigh's conifer biome forest-edge biocies are here, the sparrow being tolerant of both conifer and broad-leafed habitats, whereas the warbler occurs only in broad-leafed cover. There is of course no hard line between tall shrubbery and young tree cover, and many successional stands show a mixture of birds from both types, the relative dominance depending on the proportions of cover of various heights and densities.

2.5. Other species

Some of the wide-ranging birds mentioned under conifer forests (e.g., Red-tailed Hawk) also occur in broad-leafed stands, where certain others are more characteristic. Of the raptors, Broad-winged Hawk, and Barred, Long-eared, and Saw-whet Owls are more typical of broad-leafed forests, whereas Great Horned Owl is almost equally at home in all forest types. Species such as Sharp-shinned Hawk and Common Crow regularly nest in broad-leafed or mixed stands, but tend to forage in more open areas, so are typical really of edge situations. Pileated Woodpeckers are perhaps more regular in broad-leafed or mixed stands than in pure conifer, but evidently they are less common in the boreal region than further south. The northern hummingbirds, Ruby-throated in the east and Rufous west of the Rockies, seem not clearly characteristic of any habitat, but their affinity for flowering shrubs suggests that broad-leafed forest edges and openings are as representative as any other.

3. Forest structure and habitat partitioning

The organization of bird communities into "foraging guilds" which exploit different ecological situations in various ways has attracted considerable attention, the work of MacArthur (1958) being an outstanding example of habitat partitioning among closely related species. The weakness of most efforts of this kind is that they involve an often Procrustean attempt to classify the activities of each species into one or a few of the various categories used, whereas many birds are quite plastic in their choices, particularly when the entire geographic range of a species is taken into consideration. Thus far, this survey of boreal birds has concentrated on the major forest types, while recognizing that many bird species are not restricted to a single forest

type and some are almost ubiquitous in northern forests. I am attempting a brief consideration of foraging here, although no systematic data on this topic were collected in this study.

3.1. Forest types

First one must consider the structure of the various types of forests in the boreal region. Summaries of the tree cover of forest plots censused in this study, following James and Shugart (1970) with some additions or modifications, are given in Appendix 2 (1–4). The tree densities given for the spruce and fir plots in the eastern provinces seem too low relative to the others, but all of these were more or less disturbed by man, and I may be misremembering their true density. The vastly greater average size of trees in both British Columbia areas studied was obvious in the field as well as in the data tabulated. Schematic vegetation profiles for the major forest habitats studied — stands dominated by spruce, fir, pine, and poplar — are shown in Figure 4, based partly on data in Appendix 2. Distinctive features of each include the high canopy and lack of understorey (i.e., of regeneration) in the pioneer communities (pine and poplar), with the high concentration of shrubs under poplars, where such growth occurs mostly in spring before the canopy is leafed out; the extensive ground cover (of mosses and low or prostrate shrubs) in spruce stands; and the wide range of height classes, with a strong regenerative growth in the understorey, in the climax fir habitat.

3.2. Foraging niches

Considering only the regular birds in each major forest type (Tables 3, 5, 6, 8), it is obvious that the vast majority are partly or entirely insectivorous — this term here considered to include also those eating other common invertebrate forms such as earthworms, millipedes, spiders, and snails during the breeding season. Some turn to fruits or to seeds outside the breeding season, but these sources are of relatively minor significance during the boreal summer, except for buds, fruits, and seeds of trees, which are used extensively by the cardueline finches. Species preying on vertebrate food are rare, perhaps proportionately rarer than in more open habitats where prey species are more easily detected by a predator. Scavenging is, among birds, almost confined to the omnivorous corvids.

Compared to dietary preferences, foraging niches are less easy to define. Ground, low shrub, and canopy are almost universally accepted as distinct foraging strata; I prefer to recognize also a less clearly defined "subcanopy" stratum including tall shrubs, regeneration, and other foliage below the high canopy. Trunks and branches are also a distinct foraging stratum. However, even the most uniform stands have openings, whether from watercourses, windfalls, or man-made disturbances, and these contribute to the "subcanopy" stratum, as well as giving a quite different nature to ground and low shrub strata than is found beneath a closed canopy. The generalized vegetation profiles presented earlier (Fig. 4) should be kept in mind in the following discussion. This discussion is based on general impressions rather than systematically collected data. Some first approximations are summarized in Table 10.

Overall, aerial feeding species are of minor importance, except perhaps west of the Rockies, where the flycatchers (Tyrannidae) have diversified more than in the east. The canopy avifauna is particularly important in spruce and fir, perhaps reflecting the suggestion of MacArthur and MacArthur (1961) that different bird spe-

Table 10
Proportions of bird species (a) and individuals (b) foraging in various levels of boreal forest communities. Only regular and widely distributed species are included (cf. Tables 3, 5, 6, 8)

Forest type	(total spp. considered)	% * birds typically foraging in vegetation: On ground	Low shrubs	Sub-canopy	On trunks	Canopy	% foraging aerially
a. by species							
Spruces	(23)	30	4	9	13	39	4
Firs	(28)	29	4	11	11	43	4
Pines	(11)	50	5	18		27	
Tamarack	(9)	28	17	33		22	
Broad-leafed — E†	(23)	37	11	26	9	13	4
Broad-leafed — W†	(11)	18	9	27	4	13	27
b. by individuals							
Forest type	(Densities /100 ha)	% * birds typically foraging in vegetation: On ground	Low shrubs	Sub-canopy	On trunks	Canopy	% foraging aerially
Spruces	(200–500)	15–35	2–3	10–20	1–5	20–40	1–5
Firs	(300–600)	25–35	1–3	5–15	3–5	30–50	2–5
Pines	(125–200)	45–55	2–8	7–10		15–25	
Tamarack	(300)	13	8	26		11	2
Broad-leafed — E†	(200–450)	25–35	3–10	5–25	1–4	10–25	5–10
Broad-leafed — W†	(550)	15	3	45	1	1	10

* Some species were assigned to two categories (one-half to each), hence percentages not corresponding to whole numbers.
† E and W of Rocky Mountains.

cies exploit the inside and outside of a conifer canopy (MacArthur 1958). Birds that forage on trunks and branches are a minor element everywhere and most such species are relatively uncommon, but many are permanent residents of the boreal region. It is clear that the low shrub, and especially the subcanopy strata are much more important in deciduous stands (including tamarack) than in evergreen conifers. In fact, more both of species and of individual birds frequent the subcanopy than the high canopy of most such deciduous stands. In the boreal region, most broad-leafed stands are strictly successional, so it may not have been worthwhile for many species to specialize in the high canopy; the only common species, Red-eyed Vireo, is also ubiquitous in more southern broad-leafed stands in the east. Species frequenting the subcanopy would have had also many opportunities with successional vegetation in openings in otherwise coniferous stands. Few species frequent the low shrub stratum and only in small numbers. Finally, ground-foraging species were relatively important everywhere, but most particularly in jack pine stands, which almost lack shrub and subcanopy layers. Ground species were least important in tamarack, where the ground is very wet, and in broad-leafed stands west of the Rockies, where the shrub layer is particularly dense.

Overall, the (climax) fir community has the highest number of species and the highest density of breeding birds, presumably because, as a self-regenerating community, it shows a generally wider spread of ages and also of species of trees, and thus provides more niches for different species (Fig. 4). Mixed coniferous-deciduous stands also generally exhibit both high density and diversity. Probably old-growth spruce stands (La Roi 1967) would be roughly comparable, but as spruce is more valued as timber than is fir, such stands seldom have survived in accessible areas; most of the spruce stands that have been censused are younger and often rather even-aged, so they exhibit a more closed canopy with less stratification, fewer niches, and both lower density and number of bird species. Broad-leafed stands, though successional, typically occur on the richer sites, whereas succession on sand and rock leads usually to jack pine. Through leaf-fall, broad-leafed stands annually recycle nutrient minerals to the soil, which thus continues its relative fertility rather than becoming ever more acid and infertile as under northern conifers; the relatively high bird density and diversity probably reflect this fertility. The low species number for western broad-leafed stands may not be representative, as few such stands have been studied.

3.3. Partitioning

The partitioning of boreal forest habitats among the bird species found there thus reflects their structural simplicity in contrast to temperate and tropical forest habitats (Boughey *in* Baldwin *et al.* 1962). The scarcity of aerial-feeding species probably reflects the limited season in which flying insects are available. Spruce and fir trees offer less in the way of exposed trunk and branches than do broad-leafed trees and pines, and few birds have specialized in this foraging stratum here; this may also reflect the fact that many trunk-foraging species (woodpeckers, chickadees) are permanent residents, and the boreal winter must still further restrict opportunities for such birds (see also Distribution of boreal birds: 2. Seasonal distribution and its consequences). Most boreal birds feed either in the canopy of climax stands, or the subcanopy of successional types, or on the ground. And nearly all are specialized to exploit the seasonally abundant insect populations of the boreal summer.

I now return to consideration of the other major habitats within the boreal region.

4. Open habitats

The northern conifer biome is basically a forested region, but it includes large areas in which a tree canopy is lacking or highly fragmented. These open habitats are often merely early stages in succession which, for various reasons, persist long enough to have a distinctive bird community. Here we consider the few relatively permanent open land habitats of the boreal region, i.e., the early stages of the xerosere (Table 1), a few edge situations, and a number of miscellaneous types. Most birds associated with such situations are also found in other habitats or biomes. Those associated with aquatic succession (the hydrosere, see Table 2), which persists much longer on a given site, are discussed in Birds of the boreal region: 5. Wetlands and riparian habitats.

4.1. Permanently open

Within the boreal region, only a few land areas naturally and permanently lack a tree cover. These all have climatic and/or soil conditions in which trees cannot become established, such as very thin soils over bedrock, or very exposed slopes where sun or wind cause desiccation, or simply very low local precipitation. Such areas are common elsewhere, in the prairies, the mountains, and in the tundra region, and their occurrence in the boreal region makes possible the presence of some birds of these other biomes, even though they are far removed from the main areas of such habitats. I include here both unvegetated areas and natural grasslands; the former may be expanded for our purposes to include temporary, but recurring and often extensive, areas such as river gravels and sand barrens, which share some of the same birds. Birds of these habitats include mainly the more tolerant species found primarily in the open biomes:

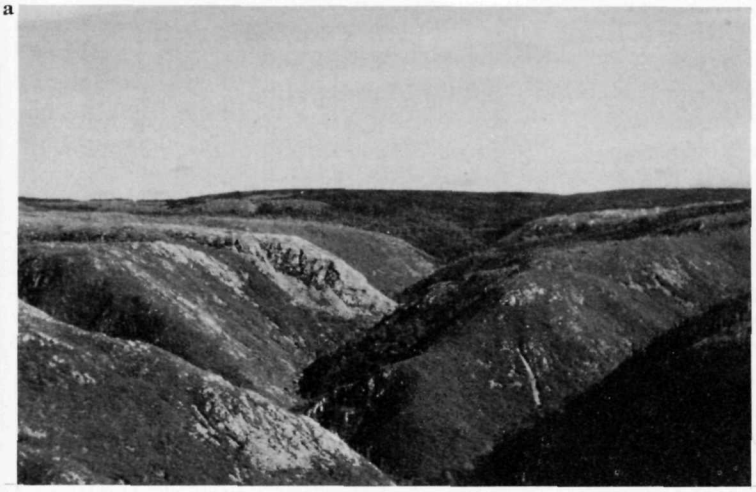
> Canada Goose (river gravels), Sharp-tailed Grouse (grasslands), Killdeer, Upland Sandpiper, Common Nighthawk, Horned Lark (very scarce), Savannah Sparrow, and Vesper Sparrow.

Some of these species are widespread and occur in other relatively open habitats, including those of the hydrosere.

Plate 11
Naturally open habitats are scarce and usually only temporary in the boreal region, which is basically a forested area — a) fire barrens (Nova Scotia); b) river gravel bars (British Columbia); c) abandoned fields (Quebec).

Plate 11

a



b

c

4.2. Burned or clearcut

In Canada, I know of no bird studies, whether using census plots or other methods, specifically covering birds of the earliest stages of forest succession (Haapanen 1965, Ferry and Frochot 1970). Although Horvath's (1963) study included several areas burned less than 20 years earlier, Martin (1960) had no upland census plots in stages earlier than the "pioneer forest" of poplar and birch. As already outlined (Table 1), the sequence on burned or clearcut areas usually goes from bare ground to shrubbery with no distinct intervening phase dominated by herbaceous vegetation. Fireweed and bracken may provide almost complete cover by late summer for a year or two before shrubs and tree regeneration begin to play a dominant role, but these do not provide cover for nesting birds during May and June; no nesting birds are clearly associated with this very transient phase. No birds are restricted to the early shrub stages of succession either, most found there being also regular in openings or understorey of older conifer stands or in shrubby bogs. As long as snags and stubs stand, Common Flickers and Olive-sided Flycatchers are characteristic of such areas, and American Kestrels and the few Mountain Bluebirds to be seen in the boreal region away from the mountains and the poplar parklands are also seen here, presumably depending on the Common Flickers for nest holes. The more generally distributed birds include:

> Hermit Thrush, Mourning Warbler, Common Yellowthroat, American Goldfinch, Northern Junco, and White-throated Sparrow.

These species, most of which forage on the ground and nest there or in nearby shrubbery, probably depend on a layer of humus and/or litter at the soil surface, this having either survived the fire or cutting, or redeveloped subsequently. Birds which forage in the shrubbery or in the air above it are less restricted. The following occur in the early shrubby stages of succession, as well as in various edge situations elsewhere, as long as their other requirements (e.g., for nest sites) are met:

> Eastern Kingbird, Eastern and Say's (west only) Phoebes, Alder Flycatcher, Tree Swallow, House Wren, American Robin, Townsend's Solitaire (west only), Bohemian (north and west only) and Cedar Waxwings, Rusty Blackbird, and Song Sparrow.

A number of others do not appear at this stage unless a ground cover of grass is present, e.g., after abandonment of old fields, chief among these being Starling and Savannah Sparrow, the former also needing tree holes nearby. Which birds appear later in the succession is determined to a large extent by whether aspen and birch or jack pine dominate the stand. Of the more generally distributed species, only Common Yellowthroat is confined to the shrub phase, although Mourning Warbler also would drop out if the succession went to pine; the others would persist longer in either successional sequence.

West of the Rockies, a number of strictly western forms occur, as noted in

previous lists. Some other species are replaced by closely related forms, for example:

Red-shafted vs. Yellow-shafted Flickers, MacGillivray's vs. Mourning Warblers, and Oregon vs. Slate-coloured Juncos.

In addition, Common Yellowthroat seems not to occur in upland succession anywhere in the west.

4.3. On the edges

Edges between habitats, particularly between closed forests and relatively open areas, are extremely varied, and the birds associated with them include many of the most common, widespread, and adaptable species which are familiar even in man's most artificial areas (see Birds of the boreal region: 6. Artificial environments). The most obvious examples are American Robin and Song Sparrow, but there are many others which nest in trees or shrubs and forage in open areas of various kinds. Some require open areas of considerable extent, e.g., American Kestrel, Common Crow, Black-billed Magpie, and Starling, whereas others are content with small openings in forest, or even simply an open understorey, e.g., Common Flickers. Many species already mentioned as frequenting the shrubby stages of succession, as well as those discussed later as associated with riparian situations (see Birds of the boreal region: 5. Wetland and riparian habitats), also occur in some edge situations.

A special group of edge birds is those that feed on flying insects. We have already mentioned the various flycatchers (Tyrannidae) found in old burns and similar open areas with elevated perches, and a few others are associated with the more open stands of conifers (Yellow-bellied and Hammond's Flycatchers) or broad-leafed trees (Pewees, Dusky Flycatcher) or with an open subcanopy in broad-leafed stands (Least Flycatchers). There are also three groups — the goatsuckers, swifts, and swallows — that feed while on the wing, and thus are not dependent on perches from which to sally out. Their distribution is influenced especially by that of a substrate appropriate for their nests, as follows:

Common Nighthawk (open areas with bare soil); Chimney (largely south of boreal region) and Vaux's Swifts (hollow trees, hence old forests); Black Swift (cliffs, western mountains only); Tree and Violet-green Swallows, Purple Martin (tree holes, hence forest or at least scattered trees); Bank Swallow (earth to sandstone banks); Cliff and Barn Swallows (cliffs or caves).

Many of these also use artificial substrates or those altered by man for nesting (see Birds of the boreal region: 6. Artificial environments; and for a fuller discussion of the swallows, see Erskine, unpublished ms.). Although Black and Vaux's Swifts and Violet-green Swallows are strictly western, the others are more or less cosmopolitan in distribution, though often very local.

Finally, open habitats also occur at the edges of the boreal region where this grades off northward into tundra and southward into prairie. Both these ecotonal regions have a number of birds largely exclusive to them, as well as others also found in similar-appearing habitats resulting from forest succession. The timberline community in mountainous areas is a special case of the tundra–forest ecotone, but also has a few distinctive species. Characteristic birds of the tundra (T) and alpine (A) ecotones with boreal forest include:

Willow Ptarmigan (TA), Sharp-tailed Grouse (T), Common Flicker (TA), Canada Jay (A), Clark's Nutcracker (A), American Robin (TA), Gray-cheeked Thrush (TA), Northern Shrike (T), Bohemian Waxwing (TA), Yellow Warbler (T), Yellow-rumped Warbler (TA), Northern Waterthrush (T), Wilson's Warbler (TA), Common Redpoll (T), Pine Siskin (A), Savannah Sparrow (TA), Northern Junco (TA), Tree Sparrow (TA), Chipping Sparrow (A), Brewer's Sparrow (A), Harris' Sparrow (T), White-crowned Sparrow (TA), Golden-crowned Sparrow (A), and Fox Sparrow (TA).

Of these, Sharp-tailed Grouse, Common Flicker, American Robin, Yellow Warbler, Savannah Sparrow, and Chipping Sparrow are also characteristic of the prairie–forest ecotone, which also features:

Eastern Kingbird, Least Flycatcher, Black-billed Magpie, House Wren, Starling, Red-eyed Vireo, Baltimore Oriole, Brewer's Blackbird, American Goldfinch, Clay-coloured Sparrow, White-throated Sparrow, and Song Sparrow.

Comparison of these lists shows Chipping Sparrow in only the prairie and alpine ecotones, perhaps limited by climate, or competition with Tree or Brewer's Sparrows, to the northward. Only Yellow Warbler appears in both prairie and tundra ecotones, but not in the subalpine where its typically riparian habitat is lacking. In contrast, 13 species are given for both tundra and alpine ecotones, and the others also include some congeneric replacement between these zones, particularly in the sparrows.

4.4. Densities

Bird densities in the various open habitats considered here are low compared to those in forests, with a few exceptions. The early successional plots on dry sites mostly had from 150 to 450 pairs per km^2, depending on their uniformity, as well as on the sizes of the trees and shrubs present. In general, their densities were lower than for young, but closed, broad-leafed stands, but higher than those for later succession involving pines. Data for the ecotonal areas are too few for effective summary. We may anticipate that the tundra–forest and alpine–forest ecotones will show quite low bird densities (Gillespie 1960, Carbyn 1971, Theberge 1976), probably mostly under 200 pairs per km^2, The prairie–forest ecotone is probably more comparable to the early successional samples (Flack 1976).

5. Wetlands and riparian habitats

Because birds of wetlands include some of the most common game species, these have received more attention than have most land birds. However, the total composition of wetland bird communities and their population densities have received as little or less study in Canada than those of most terrestrial communities. This in part is because they are less evenly distributed and thus less easily sampled in a quantitative fashion (Erskine 1968*b*, Bell *et al.* 1973). In contrast to the other descriptive sections, this chapter is not based primarily on sampling by bird census plots, but rather draws on a variety of qualitative and semi-quantitative methods. It is an extension of ideas I advanced earlier (Erskine 1971*b*) for grouping birds in and around wetlands of Cape Breton Island, Nova Scotia, but without the consideration of salinity and tidal effects associated with the sea in that study.

We earlier discussed the hydrosere (see Table 2) as a type of succession leading from open water through bog to coniferous forest. We here consider also other gradations between open water and terrestrial communities. These reflect chiefly the relative levels of water and land, and the amount and kind of vegetation growing thereon. But it must be remembered that many birds characteristic of wetland communities nest some distance away on dry land, often in a plant community in no way associated with wetlands. For example, in 1972 a Mallard nested successfully in the middle of my study plot in young jack pine forest, one of the most xeric of forest types, at least 400 m from the nearest brook and twice that from any marsh or larger water body. Remarks made earlier about variations in bird communities on land apply as much or more here. We now consider the various communities, starting from open water.

5.1. Deep marsh

Of the water birds, those that build floating nests (usually anchored to aquatic vegetation) and seldom go ashore for any purpose are at one extreme. These, with some others that build nests in the vegetation over water, make up the bird community of what is often termed (emergent) deep marsh (Millar 1976), characterized usually by permanent open water (depth 1–3 m) surrounded or interspersed with stands of reed, bulrush, or cattail. Birds found only or primarily in such situations include:

> Eared and Western Grebes, Redhead, Canvasback, Ruddy Duck, Long-billed Marsh Wren, and Yellow-headed Blackbird.

A number of other species found also in less deep and fertile marshes reach their highest densities in the deep marsh:

> Red-necked and Horned Grebes, American Coot, Franklin's Gull, Black Tern, and Red-winged Blackbird.

Most of these species are entirely or largely restricted to the marshes of western Canada, particularly those of the prairies, and their extension north into the boreal region involves few and widely scattered localities. Those species that are more widely distributed have been able to make use of other wetland habitats. Passerines are notably scarce (one wren, two blackbirds) in this group, in contrast to the number of passerines characteristic of reedbeds in Eurasia, but the Red-winged Blackbird is almost ubiquitous in boreal as in more southern wetlands of Canada. Its adaptation to upland sites, so well known in southern Ontario and the United States, seems to be lacking in the boreal region where suitable open areas are scarce.

5.2. Open water

Another group of species spend most of their time, including foraging, resting, and preening, on open water, but these do not nest over water as a rule. They include:

> Common Loon, Greater and Lesser Scaups, Common and Barrow's Goldeneyes, Bufflehead, and White-winged and Surf Scoters.

This is a heterogeneous group linked only by their dependence on deeper open waters for feeding. Buffleheads will frequent much smaller ponds than the others, which seems appropriate for their much smaller size, while goldeneyes also frequent backwaters and slow stretches of rivers as well as lakes and ponds; suitable trees for their nesting are often more common along rivers.

5.3. Shallow marsh

There is of course no firm division between the last two groups and the birds of shallow marshes, since the more tolerant species above may occur in areas where the water surface between beds of emergent vegetation is partly or largely obscured by floating plants. Species met with here may nest in the marsh over water, at the water's edge in wetland vegetation, or farther back among land plants; there seems no need to distinguish these subgroups, since few species are confined to a single nesting situation. Birds of the shallow marshes include:

> Pied-billed Grebe, American Bittern, Mallard, Black Duck, Gadwall, Pintail, American Wigeon, Green- and Blue-winged Teals, Northern Shoveler, Ring-necked Duck, Virginia Rail, Sora, and Wilson's Phalarope.

With a few exceptions, these species are much less restricted to the Prairie Provinces than were those of the deep marsh, and some are literally coast-to-coast in distribution, though doubtless varying greatly in density.

5.4. Fen

Plant ecologists use the term fen for the situation wherein the plant cover occupies most of the surface of a wetland, the water table being virtually at the level of the land, with plant nutrients in adequate supply; with nutrients scarce, such a habitat would be termed a bog. Birds associated with fens in the boreal region (e.g., Erskine 1974*a*) include:

> Marsh Hawk, Sandhill Crane, Yellow Rail, Common Snipe, Solitary Sandpiper, Greater and Lesser Yellowlegs,

Plate 12
Wetlands are extremely varied in the boreal region, as elsewhere, but the most characteristic types are bogs — a) willow/sweet gale/sedge bog (Manitoba); b) open peat/cottongrass bog (New Brunswick); c) dry peat/black spruce bog (British Columbia); d) wet sedge/tamarack bog (Quebec); e) bog edge blending into black spruce forest (Quebec); f) floodplain slough, river ox-bow (British Columbia).

Plate 12

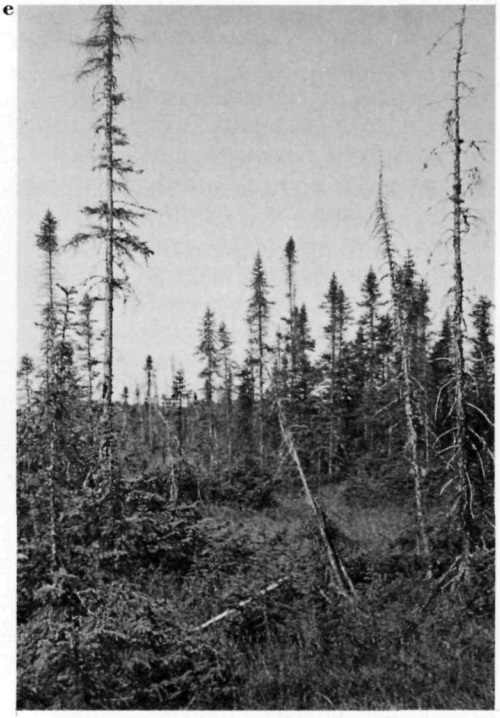
a

b

c

d

e



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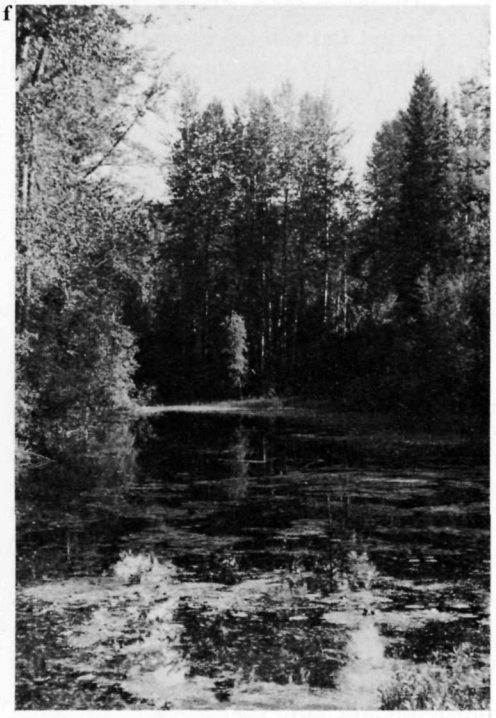


Short-billed Dowitcher, Least Sandpiper, Bonaparte's Gull, Short-billed Marsh Wren, LeConte's Sparrow, and Sharp-tailed Sparrow (*nelsoni* race only),

but the three passerines only enter the southern fringe of the region. Here too, no firm line can be drawn to separate this group from the birds of open bogs. Many species extend throughout this degree of wetness, only their relative density varying with the fertility of the habitat.

5.5. Bogs

The various wet sites collectively termed bogs have many distinct names, but by specifying the major vegetation types present we may qualify our bogs without having to define a series of specialized terms. The most open type is the raised peat bog, characterized by a rather dry layer of peatmoss with only low (10–20 cm) ericaceous shrubs, sedges, and a few herbs. This type is usually intermingled with either dry ericaceous bog, characterized by more and rather taller shrubs, or with wetter sedge meadow bog, with sedges more important. The one bird characteristic of these open bogs is Savannah Sparrow, a very widespread and tolerant species found in grassy and sedge habitats all across Canada and the northern United States, and from saltmarsh and tundra to mountain meadows (cf. the wide habitat tolerance of Meadow Pipit in Europe).

Slightly wetter areas tend to be dominated by sedges and low shrubs such as sweetgale and various willows (Table 11). Depending on the availability of open water, a variety of water birds may appear in this type, particularly:

Black Duck (E of 95°W), Ring-necked Duck, Common Snipe, Solitary Sandpiper, and Greater and Lesser Yellowlegs;

while this is perhaps the most typical wetland habitat of Short-eared Owl, which is otherwise mainly in wet fields of the prairies and similar habitats in other regions south of the boreal forest (Clark 1975).

Much the most numerous birds in this habitat, however, are passerines such as:

Alder Flycatcher, Common Yellowthroat, Red-winged Blackbird, Common Grackle, Lincoln's, Swamp, and Song Sparrows.

Common Yellowthroat and Swamp Sparrow are the most distinctive species, as the others also occur in a variety of other habitats including both wetlands and upland sites. This is perhaps the most fertile type that might be termed a bog, and it is probably more common along the southern fringes of the boreal forest than farther north.

Most boreal bogs are highly acidic owing to the acid reaction of leachings from conifer needles in the characteristic forests of surrounding areas, and in such areas stunted black spruces or tamaracks, scattered among low ericaceous shrubs with some willows or dwarf birches, are characteristic. These grade off towards the periphery of a depression into low black spruce forests (Table 2), of which the bird community was described in Birds of the boreal region: 1.1. Spruces. Characteristic birds of the more open spruce bogs (Table 11) include:

Palm Warbler, Common Yellowthroat, and Lincoln's Sparrow;

while with more or taller trees scattered in the bogs, the following may appear:

Hermit Thrush, Myrtle Warbler, Rusty Blackbird, Slate-coloured Junco, Chipping Sparrow (W of 100°W), and White-throated Sparrow (E of 90°W).

No flycatcher is found regularly in this habitat, despite the abundance of flying — and biting — insects, although Eastern Kingbirds sometimes range over such bogs from surrounding areas.

5.6. Flowing water

We may now consider the birds of flowing waters or of their unvegetated edges, and some less easily categorized water birds. In my earlier paper (Erskine 1971*b*), I remarked that of the strictly water birds only Common Merganser and Spotted Sandpiper were characteristic of flowing water, that is, of rapid rivers and streams with relatively open shores. In the western mountains, the Dipper is an obvious addition. Farther north, as the forest–tundra ecotone is approached, the Red-breasted Merganser tends to replace the Common Merganser, which in much of its range nests in hollow trees (and similarly elevated sites such as chimneys or crevices in cliffs) rather than on the ground as does its congener. None of these species except the Dipper is confined to rapid waters, though all are primarily birds of clear waters whose shores are at least in part lacking in vegetation. Belted Kingfisher and Bank Swallow, which may also be placed here, are associated with unvegetated banks and earth cliffs along rivers, as well as other shores, for nesting, though the Kingfisher also depends on water nearby as habitat for its food.

The uncategorizable species are all large and all feed primarily on fish, but have few other important resemblances. Here are such birds as White Pelican, Double-crested Cormorant, Great Blue Heron, Bald Eagle, and Osprey. Inland nesting Herring Gulls (with a few California, Ring-billed, and Mew Gulls) and Common Terns (with a few Arctic and Caspian Terns) are similarly difficult to place in any community along the hydrosere, inasmuch as they nest, rest, and preen on open, unvegetated shores, but obtain their food partly or entirely from open water. Except for the two raptors, all are colonial species which are frequently influenced by social stimuli as much as, or more than, by other environmental factors.

5.7. Riparian areas

Turning from the birds that actually make contact with the water, we find two more groups associated with the vegetation along the banks or near the shores of wetlands. The first are the birds of riparian shrubbery, all passerines except the American Woodcock, which feeds in such hab-

Table 11
Summary of data from bird censuses in bogs and fens. *Legend as in Table 3. (Two columns from* Table 3 and one column from Table 5 included for comparison.)

Species	Habitat and area											
	Sedge and low shrubs N.B.–Man. (4) [2]		Peat – low conifers Nfld.–Ont. (8) [3]		Peat – low conifers Sask.–NE B.C. (3) [2]		cf. tamarack Ont.–Man. (8)		cf. young or low spruce N.S.–Ont. (4) [1]		cf. low, sub-arctic spruce Man.–N.W.T. (7)	
Mallard and/or Black Duck	3	(3)	3	(3)			+	(1)				
Common Snipe	1	(2)	2	(4)	3	(1)					+	(2)
Lesser Yellowlegs	+	(1)			3	(2)					+	(2)
Eastern Kingbird	11	(3)	1	(1)	1	(1)	+	(1)				
Alder Flycatcher	5	(3)	4	(1)								
Tree Swallow	15	(4)	1	(1)	+	(1)					1	(1)
Canada Jay			1	(2)	2	(3)	+	(1)	2	(2)	4	(5)
Hermit Thrush			2	(1)	5	(2)	+	(2)	14	(4)	4	(2)
Swainson's Thrush			2	(1)	3	(1)	+	(1)	12	(3)	12	(5)
Ruby-crowned Kinglet			2	(2)			+	(2)	14	(3)	6	(5)
Magnolia Warbler			1	(2)			5	(4)	36	(4)	+	(1)
Myrtle Warbler			1	(1)	7	(1)	14	(5)	25	(4)	21	(7)
Blackpoll Warbler			13	(1)					1	(1)	14	(6)
Palm Warbler			4	(5)	23	(3)	+	(1)	7	(2)	3	(2)
Common Yellowthroat	138	(4)	52	(3)			20	(6)	29	(4)		
Red-winged Blackbird	20	(3)										
Rusty Blackbird			3	(3)	5	(1)			1	(1)	4	(3)
Common Grackle	3	(3)										
Purple Finch	1	(1)	+	(1)			3	(2)	2	(2)		
Savannah Sparrow	+	(1)	12	(5)								
Northern Junco			6	(2)	31	(3)	4	(5)	15	(4)	28	(7)
Chipping Sparrow					14	(3)	8	(5)			6	(3)
White-throated Sparrow			5	(3)			35	(7)	55	(4)	1	(2)
Lincoln's Sparrow			19	(5)	5	(2)	+	(3)	2	(2)		
Swamp Sparrow	199	(4)	18	(2)			2	(2)	1	(2)		
Overall mean density (range)	522 (153–709)		221 (24–465)		124 (34–253)		320 (239–469)		370 (207–468)		175 (55–240)	
Reference numbers (to Appendix 1)	I: 17, 65; III: 169		I: 18, 24; II: 122, 123, 150; III: 195, 219		II: 8; III: 174, 180		as in Table 5		as in Table 3		as in Table 3	

itats though often nesting in drier woodland nearby. Many species already met with in the shrubby sedge meadow bog type also occur here, but the most characteristic species — Yellow Warbler and Northern Waterthrush — are almost confined to this habitat in the boreal region.

5.8. Swamp and floodplain

The final category is of swamp and floodplain forests, which in the boreal region include only balsam poplar and various willows and alders of tree size, in contrast to the varied trees of more southern swamp forests. Since these stands form mainly along rivers, they tend to be narrow though sometimes of considerable length. They are typically varied habitats, often cut up by old river channels (dry in summer or holding water all year), with areas of shrubbery interspersed in openings as well as under the often high canopy, and with patches of conifers on the drier sites (e.g., Erskine, 1974*d*, Goulden 1974). Already mentioned among the birds are the tree-nesting ducks, particularly the goldeneyes and Common Mergansers (Wood Ducks and Hooded Mergansers scarcely extend into the boreal region). No bird species is confined to this type, but the more characteristic land birds include:

> Yellow-bellied Sapsucker, Eastern or Western Wood Pewees, Olive-sided Flycatcher, American Robin, Veery, Solitary Vireo, Parula Warbler, Yellow Warbler, Northern Waterthrush, Mourning or MacGillivray's Warbler, Canada Warbler, American Redstart, Rusty Blackbird, Western Tanager, Song Sparrow.

Owing to their varied nature, and also their high fertility arising from annual replenishment of nutrients through (spring) runoff flooding, these are among the richest habitats for birds as well as for other animals and plants.

5.9. Densities

We have few representative census data for most of the water birds in the boreal region, most of these arising from single species studies. For example, from data given by Vermeer (1973) one may estimate roughly one pair of Common Loons per 250 km² in central Alberta, and from Whitfield *et al.* (1974) a density of about one pair of Bald Eagles per 140 km² in central Saskatchewan. These include only the adult population and not the several year-classes of (non-breeding) subadults. Data for breeding ducks are more generally available, particularly from aerial surveys, but such results are not very comparable to those obtained by other methods. Density data are almost confined to passerines, and even these are probably unrepresentative, as wetland birds are very difficult to census accurately. Very high densities have been reported for a few bogs near the southern border of the boreal forest (e.g., Martin 1960, Brewer 1967); these were in the range from 400 to 700 pairs per km², but were based on small plots, often with exceptionally high densities of a few species (e.g., Common Yellowthroat, and White-throated, Swamp, or Song Sparrows). A sizeable sedge–shrub meadow plot I censused in Manitoba showed an exceptional density of Short-billed Marsh Wrens. No other northern plots had densities over 300 pairs per km², and most boreal bogs had fewer than 100 pairs per km², ranging down to 25. The great variations found are partly explained by the great variations in fertility and extent of tree cover, but differences in interpretation of data — especially on small plots — could have had some influence.

6. Artificial environments

In the boreal forest as elsewhere, modern man has actively modified the environment to suit his immediate needs. Birds and other organisms, and people too, have had either to adapt to the altered environments or to move away; and some have met the challenge, while others have departed. In this chapter we consider birds of artificially cleared areas and of urban developments.

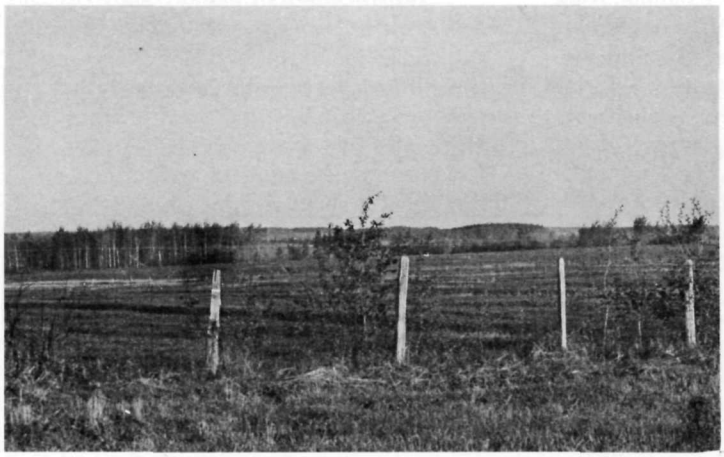
6.1. Farmland

Burns caused by man without deliberate intent have not been distinguished from natural (lightning) fires, and thus were covered in Birds of the boreal region: 4. Open habitats. Next to fire, the most extensive changes caused by man have been in the name of agriculture, although with short growing seasons and usually acid, infertile soils, the boreal forests have been less attractive for farming than most southern areas. The greatest forest area affected by this development in Canada is in southern Ontario and the St. Lawrence valley of Quebec, where the original forest cover has virtually disappeared (Edwards 1969). These areas are south of the boreal region, but the same effect may be seen in patches and strips all along the southern fringes of the boreal forest. For example, the prairie–forest ecotone, across large areas and especially in Saskatchewan, has been greatly reduced, so that now open grainlands abut on the closed forest, with no intervening parkland of shrubs and groves and clumps of poplars. Farther into the boreal region, it has been mainly the more fertile areas — valley bottoms and warm, south-facing slopes — that have been cleared, and the total area is relatively insignificant. The Clay Belt of central Ontario and Quebec deserves special mention as one of the larger areas cleared for agriculture within the boreal forest. The soils there were much more level and less rocky than in the contorted uplands of the Canadian Shield just to the south, and large areas were opened for agriculture in the 1920's and 1930's. But at latitude 48–49°N this region lacks the long growing days that permit productive grain farming in the Peace River region (lat. 56°N) of Alberta, and in the area downwind of James Bay it receives killing frosts well into June, so its growing season is short, and agriculture has proved quite uneconomical. The short growing season has also slowed reversion of the cleared land, and there are still large areas of poor fields or of old field succession here.

Plate 13
Artificial habitats represent efforts to shape the boreal region to human purposes — a) pastures and hayfields are the most extensive agricultural lands (Quebec); b) roadsides increase the available edge by providing a strip of cleared land through the forest (British Columbia); c) frontier towns often spring up like mushrooms through extensive use of mobile homes (British Columbia); d) commercial districts of northern towns are as barren as those farther south (Manitoba); e) even in long-established towns, the short growing seasons and winter cold and snow greatly restrict the development of vegetation in boreal urban habitats (British Columbia).

Plate 13

a



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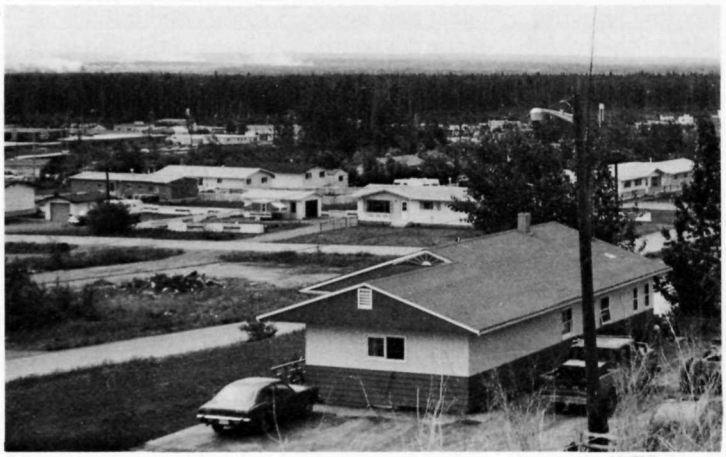

d

e

The bird community of these artificial grass and shrub lands differs little from those of the natural open areas in the same region. The characteristic species include:

American Kestrel, Killdeer, Alder Flycatcher, Barn Swallow, Common Crow, American Robin, Starling, Yellow Warbler, Common Yellowthroat, Bobolink (E from 95°W), Brewer's Blackbird (W from 95°W), Common Grackle (E from 95°W), Brown-headed Cowbird, American Goldfinch, Savannah Sparrow, Vesper Sparrow (mainly W from 95°W), and Clay-coloured Sparrow (W from 95°W).

Most of these are associated with the remnants of shrubby vegetation or tree cover rather than solely with the bald farmland aspect. Savannah Sparrow may be the only breeding bird in much northern grassland where wire fences provide the only elevated perches, as Horned Larks — the other continent-wide open country species — seldom breed in northern farmlands, most of which may be individually too small in area (cf. Oelke 1968 for the Skylark). The Barn Swallow and others of its family are special cases in that they have taken advantage of man's actions in widening their choice of nesting substrates rather than altering their preferred habitats in a wider sense (Erskine, unpublished ms.).

Table 12
Summary of data from bird censuses in urban areas. (Data from one non-boreal urban area included for comparison; all censuses by author)

	Area				
Species	Senneterre, Que.	Swan River, Man.	Fort Nelson, B.C.	Smithers, B.C.	cf. Ottawa (inner suburbs) Ont.
Rock Dove	vis.*	vis.	vis.	—	2
Common Flicker	—	3	2	—	—
Alder Flycatcher	—	—	12	—	—
Violet-green Swallow	—	—	—	96	—
Tree Swallow	180	6	30	13	8
Barn Swallow	vis.	—	—	20	—
Cliff Swallow	47	—	vis.	81	—
Purple Martin	—	—	—	—	9
Black-capped Chickadee	—	—	1	2	1
House Wren	—	40	18	—	—
American Robin	33	63	27	13	34
Cedar Waxwing	—	6	—	vis.	4
Starling	120	—	6	22	29
Red-eyed Vireo	—	—	3	—	vis
Yellow Warbler	10	9	18	vis.	—
House Sparrow	97	412	17	37	132
Red-winged Blackbird	—	—	—	—	2
Baltimore Oriole	—	—	—	—	6
Common Grackle	vis.	vis.	—	—	8
Brown-headed Cowbird	—	6	—	—	6
Pine Siskin	vis.	6	15	89	—
American Goldfinch	vis.	vis.	—	—	9
Chipping Sparrow	20	54	21	24	14
Lincoln's Sparrow	—	—	6	—	—
Song Sparrow	13	6	—	—	14
Total density overall	538	609	184	411	278
Reference number (to Appendix 1)	II: 124	III: 170	III: 181	III: 226	IV: Erskine

*vis. = visitor

6.2. Rights-of-way

Besides agricultural clearing, man has also cleared boreal forest lands for rights-of-way of roads, railways, power lines, and more recently pipelines for gas or oil. The areas occupied by roads and railways are much less than in more settled areas farther south, but they do provide corridors of open habitat which may assist spread to new areas (more important for mammals and especially plants than for birds), although the increased edge is probably significant to more birds than is the actual cleared area. The birds most obviously associated with right-of-way developments in the boreal forest are probably Savannah Sparrows along the grassy and weedy shoulders, Alder Flycatchers and Mourning Warblers in the shrubby forest edges, and Barn Swallows nesting under the bridges and culverts.

6.3. Urban areas

Last among the artificial habitats in the boreal region, but perhaps of greatest human interest, are the urban settlements. Canada has no large cities in the boreal region, the largest being Chicoutimi and Jonquière (60,000 approx.), Québec, but towns of from 2,000 to 20,000 inhabitants are scattered from Gander in Newfoundland to Whitehorse in Yukon Territory. These frontier towns show the characteristic features of most Canadian urban centres in still more extreme fashion, since the vegetation is so much governed by climate. Trees are relatively few and slow-growing, shrub cover is very limited except for a few clumps and hedges; lawns barren of all plants save introduced grasses are favoured,

Distribution of boreal birds

and flower beds are small and late-blooming. Buildings are largely of wood, the older ones providing an abundance of ledges and crannies acceptable as nest sites for some birds, and few buildings rise above two storeys even in the town centre. The birds are a mixture, including introduced species pre-adapted to man-altered habitats, plus birds using buildings for nesting, but foraging aerially or elsewhere, and widespread, tolerant species (Table 12), as follows:

> Rock Dove (introduced), Violet-green Swallow (W of Rockies), Tree Swallow, Barn Swallow, Cliff Swallow, Common Crow, House Wren (Manitoba to Rockies), American Robin, Starling (introduced), Yellow Warbler, House Sparrow (introduced), Pine Siskin, Chipping Sparrow, and Song Sparrow.

The abundance and variety of swallows is noteworthy, presumably reflecting an abundance of flying insects in and around frontier towns, as well as the nesting opportunities within them. Swallows seem to have decreased greatly in towns in southeastern Canada, perhaps from a lack of food nearby owing to air pollution or use of toxic chemical sprays. The limited availability of trees and shrubs in new residential areas, as well as commercial areas, severely restricts the numbers of many native birds there, but those able to use buildings may achieve high densities.

Overall densities of birds in northern towns vary directly with time since development and inversely with latitude, ranging from 200 to 600 pairs per km^2. Generally, censuses in towns showed densities as high as or higher than in any of the nearby natural communities studied, but usually with fewer species than in wooded habitats.

1. Distribution patterns and community structure

In the preceding sections we have looked at the composition of the bird communities in the various habitats of the boreal region. At various points we have noted that certain species were confined to certain parts of the boreal region, though their habitat might be more extensive. We will now look at distribution patterns of boreal birds, including those that also occupy adjoining regions, in hopes of gaining further insight on the origin and evolution of the boreal avifauna.

1.1. Bird faunas

There have been few attempts to look at distribution patterns across the whole of Canada, Udvardy's (1963) paper summarizing the bird faunas of North America being one of the most recent. We must keep in mind that in zoogeographic terms the fauna of a region such as Canada's boreal forest will not include all birds of all the communities there, since some will be representatives of other faunas such as those of the arctic tundra or of the eastern deciduous forest. Udvardy's outline included only the passerines, and among these he omitted a list of the species he considered to be cosmopolitan and thus not helpful in defining faunas. The birds already discussed as members of communities within the boreal region include, expectably, all 41 species of Udvardy's Boreal Forest Fauna, and 12 of 17 species of his West Coniferous Forest Fauna (missing several of the coast forest group, which was deliberately excluded from the boreal region as here defined). More instructive is the inclusion of 17 of 19 species in Udvardy's Eastern Ecotone Fauna, that is, of species common to both the eastern boreal forest and the transition zone to the south of it; and 6 of 14 species, including the whole northwestern arid-woodland group, of his Great Basin Fauna. There are also a few species listed under other faunas, but actually associated principally with the ecotones between these and the boreal forest, thus: Arctic (7 of 19 spp.), Alpine (1 of 4 spp.), Western Woodland-edge (2 of 6 spp.), Prairie (1 of 7 spp.), and Eastern Deciduous (5 of 28 spp.) faunas. Some of these overlaps are caused by the often arbitrary nature of some of Udvardy's groupings, but many others are clearly borderline cases. We could doubtless amplify the samples considerably by including the non-passerines, but it seems doubtful that the overall impression would be much altered. Overlap with adjoining regions is most important to the southeast, less so to the southwest, and to a very minor extent with the open habitats to the north (tundra) and south (prairie), which is hardly surprising since we defined the boreal region as a forested zone.

1.2. Evolution

Aside from the biogeoclimatic differences between biomes, the evolutionary history of each species may decide whether it is found in only one or throughout several biomes. In particular, the successive contractions and expansions of ranges in response to the Pleistocene glaciations resulted in fragmentation and subsequent meeting, with or without merging, of the segregated forms, sometimes resulting in speciation (Moreau 1966, Haffer 1974). Mengel (1964) provided a detailed and illuminating discussion of possible evolution in the North American warblers (Parulidae), later somewhat modified by Hubbard (1969) and Flack (1976); and Short (1965) described the post-Pleistocene meeting and introgression of the disparate forms of Common Flickers. The habitat preferences now assembled provide an additional means of recognizing which populations, whether of species or subspecies rank, have had diverse evolutionary histories. The next section considers cases where recognized species or subspecies pairs occupy different habitats in different parts of the boreal region, and also those where densities of these forms differ markedly between areas. The non-passerines contributed little to this comparison, not surprisingly as many (e.g., water birds) are obviously limited in dis-

tribution by factors other than evolutionary history, and many of these became distinct species much farther back in time.

1.3. Differences

Table 13 presents comparisons of congeneric species pairs, including a number recently merged or separated (AOU 1973). None of the cases where species were recently merged involved a break in ecological relationships, while the one case of a species being split (Traill's Flycatcher) involved a very slight ecological difference (Stein 1963). In many of the other pairs, one species was associated with non-boreal areas only, but not all of these involved clear differences in habitats. In most cases where both used similar habitats, they were generally scarcer in the regions where their ranges met or approached each other. This is not usually apparent from distribution maps or descriptions of ranges, which often take no account of relative densities in different areas. I illustrated this concept earlier (Erskine 1971c) for Common Grackle and Brewer's Blackbird. Another excellent example is the wood pewees, both of which are far less common and regular in Manitoba and adjoining areas than in their respective main ranges farther east and west. Of the 23 pairs listed in Table 13, at least two-thirds have one member confined to or most regularly occurring in the area west of the Rocky Mountains, reflecting the most obvious faunal break within the boreal region. No other pattern recurred often enough to be surely recognizable.

Subspecies might be expected to give rise to many different distribution patterns, but most areas where subspecies of Canadian birds intergrade coincide with those where other species pairs approach each other (Table 14). Presumably the populations on one side of such a dividing line had a common evolutionary history during recent geological time, while those on the other side of the line shared a common history differing from the former group. One of the most common subspecific patterns involves a distinct race inhabiting the humid

Table 13
Congeneric species pairs* and their relationship to bird communities. Species not breeding in boreal region in parentheses

Species	Major habitat(s)	Rel. density in Can. range
Mallard	Shallow marsh (in prairie & forest)	Common in W; scarce in E
Black Duck	Shallow marsh (in forest)	Fairly common in E only (reduced by hunting?)
Common Goldeneye	Deep marsh to open water (in forest)	
Barrow's Goldeneye	Same	Comparable
Red-tailed Hawk*	Conifer and mixed forest	
Harlan's Hawk*	Same	Comparable
Greater Yellowlegs	Fen and bog	
Lesser Yellowlegs	Same	Comparable
Barred Owl	Mixed and broad-leafed forest	Common in E; scarce in W
(Spotted Owl)	Mature conifer forest	Scarce in W only
(Chimney Swift)	Mixed and broad-leafed forest (originally)	Common in E only
Vaux's Swift	Conifer forest	Scarce in W only
Ruby-throated Hummingbird	Broad-leafed forest edge	Fairly common in E only
(Black-chinned Hummingbird)	Conifer forest edge	Scarce in W only
Yellow-shafted Flicker	Forest edge	
Red-shafted Flicker	Same	Comparable
Yellow-bellied Sapsucker	Mixed and broad-leafed forest	Common in E; fairly common in W
(Williamson's Sapsucker)	Conifer and mixed forest	Scarce in W only
Eastern Phoebe	Broad-leafed forest edge	Uncommon E; scarce W
Say's Phoebe	Arid woodland edge	Scarce in W only
Alder Flycatcher	Wetland-edge scrub	Comparable
(Willow Flycatcher)	Wet and dry edges and scrub	
(Eastern Wood Pewee)	Broad-leafed forest edge	Common in E; scarce in W
Western Wood Pewee	Broad-leafed and mixed forest edge	Scarce in E; common in W
Blue Jay	Mixed and broad-leafed forest and edge	Common in E; scarce in W
Steller's Jay	Conifer and mixed forest	Scarce in E; common in W
Common Crow	Very varied, including coastal (except W coast)	Very common
(Northwestern Crow)	Coastal	Very common in W only
Boreal Chickadee	Conifer forest	Fairly common in E; scarce in W
(Chestnut-backed Chickadee)	Conifer forest	Scarce in E; common in W
(Eastern Bluebird)	Broad-leafed forest edge	Scarce in E only
Mountain Bluebird	Broad-leafed forest edge	Scarce in E; fairly common in W
Myrtle Warbler*	Conifer forest	
Audubon's Warbler*	Conifer, mixed, & broad-leafed forest	Comparable
Black-throated Green Warbler	Conifer and mixed forest	
Townsend's Warbler	Conifer forest	Comparable
Mourning Warbler	Broad-leafed forest edge	
MacGillivray's Warbler	Same	Comparable

cont'd. on page 52

Table 13 *cont'd.*

Species	Major habitat(s)	Rel. density in Can. range
Rusty Blackbird	Conifer forest bogs	Scarce in W; fairly common in E
Brewer's Blackbird	Broad-leafed & mixed forest edge	Common in W; scarce in E
Rose-breasted Grosbeak	Mixed and broad-leafed forest	Fairly common in E; uncommon in W
(Black-headed Grosbeak)	Mixed and broad-leafed forest	Scarce in W only
Purple Finch	Conifer and mixed forest and edge	
(Cassin's Finch)	Open conifer forest	Comparable
Slate-coloured Junco*	Conifer and mixed forest edge	
Oregon Junco*	Same	Comparable

* Including some (marked *) recently merged or separated.

Table 14
Subspecific variations in habitat preference or density

Species	Comments (source in parentheses)
Sharp-tailed Grouse	3 prairie races (incl. *columbianus* in B.C.) are quite common; 3 boreal-subarctic races much scarcer (my observations)*
Yellow-bellied Sapsucker	Sedentary west coast race (*ruber*) generally scarcer than other two races (my observations)
Black-capped Chickadee	B.C. interior (*fortuitus*) and coast (*occidentalis*) races attain much higher densities than those E of Rockies (BBS)*
Boreal Chickadee	B.C. interior (*columbianus*) race rare compared to eastern races (my observations)
Brown Creeper	B.C. coast race (*occidentalis*) much more common, and interior B.C.–Alta. race (*montana*) much scarcer than widespread eastern form (BBS, census plots*, my observations)
Hermit Thrush	Widespread eastern race (*faxoni*) generally more common than 3. B.C. races; habitats of *faxoni* well-defined, of B.C. races uncertain (census plots).
Swainson's Thrush	Eastern race (*swainsoni*) mainly in spruce/fir; interior B.C. (*almae*) and Yukon (*incana*) races also in pine and poplar — in fact, in all forests; coastal race (*ustulatus*) in all forests (census plots)
Veery	Only northeastern race (*fuliginosa*) appreciably penetrates the boreal region, other races only in southern ecotone and southward, generally at much higher densities (BBS)
Golden-crowned Kinglet	Eastern race (*satrapa*) regular in fir and spruce, except not in fir W of Ontario; interior B.C. race (*amoenus*) in all spruce & fir; west coast race (*olivaceus*) much more common than others (BBS, census plots)
Ruby-crowned Kinglet	West coast race (*grinnelli*) rare, almost lacking; interior B.C. race (*cineraceus*) also much less common than eastern race (BBS, census plots)
Warbling Vireo	Eastern race (*gilvus*) does not enter boreal region, whereas western race (*swainsoni*) is the common vireo N of 53° in B.C., in closed as well as the more open broad-leafed stands frequented by *gilvus* (BBS, census plots, my observations)
Orange-crowned Warbler	All races frequent broad-leafed understorey in largely conifer regions, but eastern race (*celata*) is rare whereas both B.C. races are common (BBS, census plots, my observations)

cont'd. on page 53

coast forest region of British Columbia, whether the rest of its Canadian range is occupied by one race (e.g., Great Blue Heron) or several races (e.g., Hermit Thrush). Another very common division, as with the species pairs, is along the line of the (southern) Canadian Rockies; in such cases, the eastern form may extend on through Yukon Territory to Alaska (e.g., Ruby-crowned Kinglet), or there may be a separate northwestern race (e.g., Boreal Chickadee). Interior British Columbia may be occupied by an eastern race (e.g., Brown Creeper), but much more often by one or more forms distinct both from the eastern and west coast races (e.g., Golden-crowned Kinglet); and the divisions within this intermountain region vary from latitude 50° to 56°N, though most commonly approximating a line from Kitimat to Banff, and thus roughly corresponding to the southern edge of the boreal region as here understood. Farther east there are few recurring divisions, but a number of species show racial separation in the area between Lake Superior and Hudson Bay. Insular races on Newfoundland are also frequent, but there are few named forms from the Maritime Provinces. It may be well to emphasize two points here: (1) sedentary (year-round resident) forms attain generally lower densities than migratory forms, since the former are limited to the numbers that the habitat can support through the winters, and (2) sedentary forms tend to show more differentiation (i.e., more races) than migratory forms, since mutations can be more easily fixed within a small, closed population.

Most of the larger non-passerines are too seldom recorded both on census plots and in the Breeding Bird Survey roadside counts to give useful density figures. These species are often wide-ranging through a variety of habitats, e.g., Red-tailed Hawk, Ruffed Grouse, but a few show interesting variations which are listed in Table 14 with those for various passerines. We would expect from basic principles that densities would be lower in regions where the energy

Table 14 *cont'd.*

Species	Comments (source in parentheses)
Nashville Warbler	Eastern & western races widely separated (only warbler so disjunct), western (*ridgwayi*) not reaching boreal region and frequenting dry, shrubby broad-leafed stands, in contrast to moister broad-leafed understorey or edge in conifer areas for eastern race, latter much more common (BBS, census plots)
Common Yellowthroat	Western races (*campicola, yukonicola, arizela*) occur only in marsh edge shrubbery, and at much lower densities than eastern race (*brachydactyla*) which also occurs in shrub stages of upland succession (census plots, BBS)
Red-winged Blackbird	Upland field breeding seems to be confined to eastern race (*phoeniceus*), and even there only south of the boreal region. All boreal populations and races strictly marsh-nesting (census plots, my observations)
Sharp-tailed Sparrow	One race (*nelsoni*) occurs inland and penetrates boreal region, where scarcer than elsewhere; other races strictly coastal and in salt marsh (BBS, my observations)
Chipping Sparrow	Western race (*boreophila*) found in most conifer and some broad-leafed habitats; eastern race (*passerina*) a forest-edge species and in (open) pine stands, not in other forests, but overall densities from roadside counts similar for both (census plots, BBS)
White-crowned Sparrow	West coast race (*pugetensis*) occupies lowland forest-edge shrubbery, and has lower density than other races which occur in subarctic or subalpine shrubbery; but some members of *gambeli* in interior B.C. also found in open woodland and forest edges at still lower densities (BBS, census plots, my observations)
Fox Sparrow	Coastal populations (*fuliginosa* in west, *iliaca* in east) attain much higher densities than other, largely subalpine or subarctic races (BBS, my observations)

* Sources (in order of preference): (1) census plots (mapping census studies), (2) BBS — Breeding Bird Survey (roadside counts), (3) my observations at other times.

flow is on the average slower, e.g., insubarctic or subalpine regions, and this is noted in several cases. For some species, still higher densities are found on the west coast, where with longer frost-free periods the overall energy flows should be the highest of any conifer habitat in Canada. However, this may be complicated by competition since, for example, the very high densities of Black-capped and Chestnut-backed Chickadees and of Brown Creepers in the Coast Forest occur in the absence of the wide variety of warblers (Parulidae) found east of the Rockies where chickadee densities are lower (Snyder 1950; contra Sturman 1968). In this context, we may note that in the west of Eurasia, where the titmice (chickadees, Paridae) are also very abundant, this is achieved at least in part by the presence in an area of a number of species rather than by very high densities of one or two species.

The few cases where different races frequent different habitats are even more striking than the differences in density, especially when equivalent habitats are present throughout the species' ranges, as with Common Yellowthroat and Chipping Sparrow. Competition may be involved in some cases, as Swainson's Thrushes are regular in broad-leafed stands only to the northwest of the range of Veeries, and Warbling Vireos are the dominant vireo only where the larger Red-eyed Vireo is absent at least in the early part of the breeding season.

Differences in evolutionary history, leading to separate species or races in different parts or habitats of the boreal region, presumably involve their having existed in separate refugia during one or more glacial maxima. Moreau (1966) emphasized that, in tropical regions, forests generally and particularly the cooler tropical montane types were more extensive in the cooler climates associated with glacial maxima in the north (pluvial periods in the tropics). This was by no means definitely the case with the types we now think of as boreal forests, which in North America were probably restricted to rather small areas in the southeast and southwest, with subarctic remnants in Alaska, at such times (Hubbard 1969). Boughey (*in* Baldwin *et al.* 1962) remarked that to a person who had worked in the tropics the term "climax vegetation" seemed a misnomer when applied to boreal forests in eastern Canada, where plant communities appeared "remarkably limited and comparatively unvarying". This of course reflects both the present harsh climate of this region and its short history on present sites, since 10,000 years ago most of Canada was under ice. There always must have been arctic and subarctic zones south of the ice edge, and Johansen (1963) emphasized the importance of the subarctic both of itself and as a feeder of species to the arctic and boreal regions. However, we would expect that species characteristic of relatively mature (climax?) forests would be more specialized and also longer adapted to these habitats, thus giving more information on evolutionary history, than those species at home in successional stages or in the subarctic zone.

In much of the boreal region, the most common and distinctive birds are wood warblers (Parulidae). In discussing this family, Mengel (1964) suggested that their original habitats were broad-leafed forest or scrub, from which some species had adapted to and been fragmented within northern conifer forest as this expanded and shrank again during the various glacial

Table 15
North American birds confined or nearly restricted to boreal conifer forests in breeding season

Species	Comments
Blue Grouse Spruce Grouse	Holarctic family; cf. Capercaillie, Black Grouse
Great Gray Owl Hawk Owl Boreal Owl	All are holarctic species
Black-backed Three-toed Woodpecker Northern Three-toed Woodpecker	Holarctic genus Holarctic species
Yellow-bellied Flycatcher Hammond's Flycatcher	Neotropical suborder and family
Canada Jay	Holarctic genus; cf. Siberian Jay
Mountain Chickadee Boreal Chickadee Chestnut-backed Chickadee	Holarctic genus; cf. Coal Tit, Siberian Tit (Gray-headed Chickadee)
Golden-crowned Kinglet	Holarctic genus; cf. Goldcrest, Firecrest
Myrtle Warbler Cape May Warbler Bay-breasted Warbler Blackpoll Warbler Palm Warbler	Neotropical family
Red Crossbill White-winged Crossbill	Both are holarctic species

Table 16
An approximate breakdown of birds occurring in Canadian boreal region, by wintering region

	No. of species (approx.)		
Grouping	Breeding in boreal region	Migrants from arctic and subarctic regions	Total
Total "boreal birds"	210	40	250
Birds wintering:			
in boreal region	35	10	45
farther south	175	30	205
Water birds wintering on coasts or south of frost line	55	25	80
Land birds	120	5	125
Land birds wintering:			
entirely north of 30°N	19	5	24
both north and south of 30°N	47		47
entirely south of 30°N	54		54*

* *Complete list in Appendix 3.*

and interglacial periods. At the same time, populations of many of these species still exist in cooler mixed or broad-leafed forests of the Appalachian Mountains, which may be more similar to their ancestral habitat than are the Canadian forests. This hypothesis seems plausible to me, and in support of it is the fact, already mentioned, that species such as Blackburnian, Black-throated Green, and Magnolia Warblers, within the northern transition or boreal forest regions, are characteristic of the most fertile coniferous situations available, whether this is hemlock, balsam fir, or white spruces amid poplars. The first two species mentioned above also attain higher densities south of the boreal forest than anywhere in it. The broad-leafed eastern forests, with their heavy leaf-fall, undoubtedly have a still higher fertility and greater energy turnover than even the richest conifer habitat, so a species pre-adapted to such a rich habitat would tend to occupy the richest one available in a new region.

1.4. Birds breeding only in the boreal region

The species largely or entirely restricted to the boreal conifer forests in North America are strikingly few, and with only few exceptions are of families also represented in the cooler parts of Eurasia (Table 15). Many are of holarctic genera and a few even of holarctic species. The exceptions, a few *Empidonax* flycatchers and *Dendroica* warblers, belong to exclusively American groups (family Tyrannidae of the suborder Tyranni, and family Parulidae) of which other northern members frequent a wide variety of conifer and broad-leafed habitats. The boreal exceptions thus are probably only secondarily adapted to conifer forest. The other boreal conifer birds probably entered North America from Siberia during interglacial periods in the past, the grouse presumably earlier than the rest since they alone have attained generic status separate from Eurasian forms (these two grouse are more

closely related to each other than to any other form; Short 1967). The three-toed woodpeckers (Short 1974) are an example of a pattern where a single holarctic species has split off a second, more southern and usually (but not in this case) smaller representative in North America, as in the scaups, the shrikes, and the waxwings. The Mountain Chickadee is evidently a secondary specialization to conifer forest of the widespread and very tolerant Black-capped Chickadee stock, but Boreal and Chestnut-backed Chickadees are closely related to the Gray-headed Chickadee (Siberian Tit). The kinglets are obvious counterparts to their Eurasian congeners.

1.5. Adaptation

Every other group of birds found in Canada's boreal region is either of neotropical origin (e.g., flycatchers, vireos, blackbirds) or shared with Eurasia (e.g., most water birds). All other land birds are associated with broad-leafed or mixed forest or with successional stages, which also may be either broad-leafed or mixed, or are tolerant of both conifer and broad-leafed habitats. There are no endemic orders or families, and even endemic genera are scarce if one makes due allowance for the excessive zeal of taxonomic splitters of past generations.

In birds, then, we come to much the same conclusion as did the botanist cited earlier for plant populations — in the boreal region they are "remarkably limited and comparatively unvarying" (Boughey *in* Baldwin *et al.* 1962). With few exceptions, our land bird fauna is of geologically recent origin, and has still more recently adapted to its present ranges and habitats. We may thus anticipate that most species will be able to cope with appreciable changes in their present environments, providing these do not occur too sweepingly or suddenly. Man's capacity for initiating sudden and sweeping environmental changes must not be underestimated, but fortunately for the birds there is still a lot of Canada which is relatively untouched and may well remain so, since the development of remote areas is rapidly becoming unfeasible from both the energy and economic standpoint.

2. Seasonal distribution and its consequences

A striking feature of bird life in the boreal region is its seasonal variation, reflecting the annual breeding activities and also a directed movement into and out of the region. These migrations are clearly related to the fact that the changing seasons make food unavailable there for many groups of birds for large parts of the year. Whether the migrations evolved to allow boreal birds to survive the harsh winter or to allow originally tropical and temperate birds to exploit boreal resources while these are briefly available has not been settled conclusively, although the latter hypothesis seems more likely. The energy flow within boreal communities has not been worked out in detail, but evidence from other biomes (e.g., Maher 1970, Holmes and Sturges 1973) suggests that birds play a very small role, as one would expect from their relatively high positions in food pyramids. Their movements into and out of the boreal ecosystem are thus of only minor influence on its energy flow, which also has an enormous seasonal fluctuation.

Our knowledge of boreal bird distribution and community structure in the breeding season, though imperfect, is satisfyingly complete in comparison to knowledge of these birds at other seasons, when they are not tied to one area by parental responsibilities. I have attempted a survey, based largely on winter ranges given in the AOU Check-list (1957), of where our boreal birds spend the rest of the year (Table 16; cf. MacArthur 1959). The more obvious weaknesses in the data include the question of whether the more northern breeding populations of wide-ranging species are concentrated in winter near the northern edge of the winter range, or near the southern edge, or are generally distributed. The winter ranges given for different subspecies (AOU 1957) suggest that many of the boreal races winter farther north than more southern breeding populations, but such data are available for few species, and the band recovery data for some species, e.g., Black Duck (Addy 1953), suggest a reverse tendency. Banding recoveries for most species are wholly inadequate to resolve this difficulty, since very little banding has been done in the boreal region. Another obvious weakness is that the winter ranges usually gave no indication whether the species was common or only casual in the peripheral areas named; census data also are inadequate to clarify the situation. Nevertheless, the broad patterns which emerged are unlikely to be seriously altered by more precise information, even though we are reduced to talking of approximate numbers of species rather than of individuals.

2.1. Wintering

Of about 250 species which breed in or migrate through the boreal region, excluding strays (Table 16), only about 45 seem to occur regularly as wintering birds. Many of these also occur to the south and a few also to the north of this region in some or all years. The majority are year-round residents* of the boreal forest, thus:

> Goshawk, Spruce Grouse, Ruffed Grouse, 7 owls, 5 woodpeckers, 3 jays, Common Raven, 3 chickadees, Red-breasted Nuthatch, Brown Creeper, Golden-crowned Kinglet, and 7 carduline finches.

The introduced Rock Dove and House Sparrow are resident where they occur, but are probably limited northward by whether they can survive the winters, e.g., by sheltering inside grain elevators and other buildings (Blem 1973). Dippers also live year-round in the rapid streams of the western mountains, where these do not freeze over completely. The other wintering species are largely associated with the

* Some or most individuals of some of these species are migratory, but others winter in the boreal region.

Plate 14
The breeding season for boreal birds is short, as snow lies well into April even in the southern parts of the region — the example shown was 8 April, 1967 (southeastern New Brunswick).

subarctic or subalpine ecotone in summer, and with the more open areas within — as well as to the north and south of — the boreal region in winter, thus:

Golden Eagle, Gyrfalcon, Sharp-tailed Grouse, Willow Ptarmigan, Snowy Owl, Black-billed Magpie, Clark's Nutcracker, Bohemian Waxwing, Northern Shrike, and Snow Bunting.

The remaining 205 (±) species, comprising about 82% of the total, and including all the 80 species of water and shore birds, leave the boreal region entirely in winter. Most species from the open tundra seek out similarly open habitats, on prairies, agricultural areas, shores, or on the oceans, in winter, and thus pass over the boreal region with few and brief pauses, if they stop there at all. The water birds, which comprise nearly 40% of the migrants, are not discussed further here.

Among the land birds, about 13 winter only in South America, 12 only in Central America, the West Indies, and Mexico, 20 in these areas plus South America, and another 9 species in the southernmost of the United States as well as farther south. In all, about 45% of the migrant land bird species of the boreal region winter in the tropics or subtropical regions, and a substantial fraction of the others winter farther north only along the west coast, where winters are also very mild. Even with all the qualifications one may wish to attach to such data, roughly half of these species – and of the individuals? — winter south of latitude 30°N, and the other half between latitude 30° and 45°N. The former group includes those that feed mainly on insects or fruit, the latter those that feed on seeds and other foods that are available in areas with less mild winters.

2.2. Migration

Few migrant species arrive in the boreal region before bare patches of ground appear in the snowy landscape, usually some time in April. Strictly insectivorous species cannot afford to arrive until almost the end of May. Most of the insect-eaters (flycatchers, swallows, vireos, warblers) are gone by early September, having spent little more than 3 months in their summer homes, and other migrants leave before mid-October, after stays averaging 4 to 5 months. Data summarized by Lincoln (1950) suggest that land birds in spring take about 6 weeks to move from the tropics to the boreal region, and the fall migration may be guessed to extend over a similar period. Thus, insectivorous birds spend 3 to 4 months on migration and 5 to 6 months in their wintering areas. The seed-eaters, which spend about 5 months in breeding areas, but have a much shorter migration, may also spend up to 5 months in the winter range. Thus, for most species which breed in or migrate through the boreal region, other more southerly regions may be much more important in their annual energy budgets. Such birds may spend less energy and/or ensure more surviving offspring by migrating north to breed, despite all the demands and hazards of migration, than by remaining year-round in the tropics where they have to partition the available resources with the species resident there. Canadians faced with the energy costs of heating their homes, cars, and work places in winter may wish to ponder the birds' example.

Plate 14

2.3. Residents

The few species which remain in the boreal region are nearly all of holarctic families, genera, or species. They include examples of most of the foraging patterns applicable in the boreal habitats in winter: herbivores (grouse), seed-eaters (nutcrackers, finches, bunting), a fruit-eater (waxwing), bark and conifer foliage gleaners — i.e., insectivores (woodpeckers, chickadees, nuthatch, creeper, kinglet), predators (hawk, eagle, falcon, owls, shrike), scavengers — omnivores (jays, Black-billed Magpie, Common Raven).

The impact of man

Those species from families which also contain migratory species are typically much scarcer than their migratory relatives: cf. Hairy Woodpecker vs. Yellow-bellied Sapsucker; Golden-crowned vs. Ruby-crowned Kinglet; Goshawk vs. Red-tailed Hawk (the resident form given first in each pair). The resident species must be limited in some way to such population densities as can be supported through the northern winter, but most of these species also are involved in emigrations in some years (Bock and Lepthien 1976), probably when breeding success and population density have been higher than usual. Such irruptive behaviour transfers a large part of the boreal population of a species into other areas both within and beyond the boreal region, where some individuals of opportunistic species such as crossbills and siskins may nest (e.g., Godfrey 1976). Even if such breeding represents only a temporary addition to the regular range, this behaviour relieves population pressure in the main boreal range of the species. A large proportion of the members of most irruptions are believed to perish, neither returning to their original range nor subsequently breeding elsewhere, but some presumably have pioneered known range expansions, such as that of the Evening Grosbeak to eastern Canada in the 20th century, or the return of Red Crossbills and Bohemian Waxwings to Nova Scotia in the 1960's after virtual absence for 40 years (Tufts 1962).

2.4. Survival

As suggested earlier by Fretwell (1972), what happens on the winter range may equal or exceed in importance what happens in breeding areas. The long-term survival of many boreal birds of Canada may be influenced more by the human population explosion and consequent clearing of forests for agriculture in Central and South America than by the rush to exploit the few untapped sources of non-renewable energy (fossil fuels) within Canada. However, the relatively meagre evidence suggests that most boreal birds wintering in the tropics frequent disturbed habitats rather than the virgin forests on which the local endemic species depend (Tramer 1974, Karr 1976). Meanwhile, back in the boreal forest region the resident species, though relatively few, are widely distributed through a variety of types and ages of forests. Many of them are not sedentary, some having a part of the population migrating while other individuals remain all year in the breeding area, and while others through irruptive behaviour are in a position to colonize any suitable area that becomes available. None is confined to mature, old-growth forest; probably no resident boreal species could afford to be so restricted in view of the frequent outbreaks of fire and forest insects which limit the extent and duration of such stands (Baldwin *et al.* 1962), and the comparatively brief period in which such biomes have occupied their present geographic positions. Collectively, boreal birds seem rather an opportunistic and adaptable group, having been able to cope with the gradual shifts of their chosen habitats over glacial epochs, as well as with sweeping seasonal movements between biomes in the course of their migrations. Their abilities to cope with the impact of man are discussed in the final section.

Man is the dominant vertebrate wherever he occurs, in the boreal forest biome as elsewhere. Nevertheless, this region is one that still springs to mind when a North American thinks of wilderness, another being mountains. Native prairie and arctic tundra are less often thought of as wilderness, presumably because wide open spaces allow one to see what else is sharing the country one is in. We now consider the boreal forest biome from the aspect of man's efforts, past, present, and future, towards civilizing what was and is often thought of as a dangerous and alien area.

The first settlers in Canada looked on the forests, whether boreal or eastern deciduous–transition, as something to be pushed back so that dangerous animals — on four legs or two — could not lurk nearby to attack them. That they also depended on the forests for fuel through the Canadian winters, as well as for many other purposes, would have seemed irrelevant to them, since these vast forests, then as now, were looked on as an unlimited resource. Exploitation of other resources of boreal Canada has followed a similar pattern with a similar outlook since then, and only in the most recent years has a concept of the finiteness of most resources on earth become widespread. The major patterns of man's actions have involved extracting minerals and petroleum, clearing forests for agriculture, cutting forests for wood and wood products, damming and diverting rivers for electricity, flood control, or canal transport, and polluting, both intentionally and heedlessly.

1. Minerals

In principle, the extraction of mineral resources should not be a significant influence on bird life, since few birds live in the ground or depend directly on minerals obtainable from the ground. The difficulties arise from the methods used in extraction, whether these involve complete devastation by strip-mining without subsequent re-

storation, or the blight associated with fumes from most major smelter operations, the disturbances from construction and use of roads, railways, or pipelines used to transport the extracted resource to where it will be used, or simply those brought about by prospecting. The total area influenced is usually only a small part of a region, although it may encompass many square miles, and the effect on birdlife of the area may be an exchange of forest birds for those adapted to open habitats, or an elimination of all birds, depending on the severity of the disturbance. Although one may deplore the kinds of devastation exemplified by Grand Cache and Sudbury, it seems unlikely that extractive mining of itself is a major harmful influence on land birds on more than a local scale.

2. Forestry and agriculture

The use of so-called renewable resources is perhaps the major effect of man in most of the boreal forest region. The destruction of forests and their replacement by some form of low herbaceous cover in the name of agriculture is quite minor in extent in the boreal region, as few areas combine the necessary soil fertility and a suitable growing season. This use cannot be dismissed as of no account, however, because the lands taken up for agriculture usually include the most fertile areas, which may support rich communities of restricted extent, possibly even with unique species of plants or animals. My impression thus far is that most sites likely to be attractive for agriculture support higher densities and greater variety of birds rather than species restricted in range or tolerance, but this may not be so for other, less mobile forms of life. Since long-term trends in climate seem to be towards less favourable conditions in northern areas (Lamb 1975), the prospects for great increases in northern agriculture seem slight, posing little threat to birds in general.

Forestry is a good example of exploitation of a renewable resource, since the ever-increasing demand for wood for a multitude of purposes has ensured that some concern be given to regeneration of forest cover in cut-over areas. Natural regeneration is often sufficient, but for accessible areas seeding or planting is used extensively to supplement natural succession, and to avoid or postpone a need for working more distant and thus more expensive sources. Modern mechanized operations require the processing of large blocks at a time, which tends to change the proportions of different stages of succession in a region. And the trend towards shorter turnover cycles, with a given area cut after a briefer interval (i.e., making use of younger age classes of trees), tends to eliminate old-growth forests altogether in areas easy of access to lumbering. A lumbering industry, except for very specialized cases such as fine hardwoods for cabinet-making, can only develop to exploit trees of considerable abundance, so scarce, late-climax trees of no great commercial value are apt to be eliminated in accessible areas. The last proviso is most important, however, since lumber in general is not yet nor likely to become sufficiently scarce in Canada to justify its transportation from remote areas, where forest succession is thus likely to follow a natural course for the indefinite future.

The most obvious cases where potential damage to birdlife might occur if communities were eliminated involve (eastern) hemlock in the northern hardwoods transition region and balsam fir in the boreal forest region west of central Quebec. These types are respectively the most fertile needle-leafed forest communities in their regions, and support a number of birds virtually lacking elsewhere in Canada. However, it may be significant that these same bird species are characteristic, not so much of a given forest community, as of the most fertile needle-leafed forest type available there. Magnolia Warblers in the Fort Nelson region occupied small groups of mature white spruces amid poplar forest, in the absence of any balsam fir, and Black-throated Green Warblers in the Peace River district occurred in riparian white spruce stands, so these birds may move only to the richest spruce types in the northeast if mature fir or hemlock ever became unavailable. Few of our boreal birds seem so narrowly tolerant as to be obviously threatened by elimination of a single scarce forest type (Mengel 1964, p. 10). Some managed forests and plantations of pines and spruces are very poor bird habitats (e.g., MacDonald 1965), but an even-aged stand of trees is seldom if ever as barren and monotonous as an agricultural crop, owing to variations in the site quality and through the long growth period required by trees.

3. Water projects

A third major class of renewable resource exploitation is the development of hydro-electric power by damming rivers and diverting others into the reservoirs so created. Regulation of water levels for canals and for flood control are other reasons advanced for damming rivers, but such regulation of water flow is quite as likely to disadvantage wildlife as to benefit it (Dirschl 1972). The results above the dam include complete loss of existing riparian communities, which are often very fertile and diverse, so the effect is greater that that of a random withdrawal of a comparable area of upland. The effect surely is greatest on water birds, as most hydro reservoirs fluctuate too greatly in level to allow development of productive marsh habitats, even where shoreline slopes are sufficiently gradual to allow this. Land birds and riparian species are less affected by dams in boreal Canada than along the rivers crossing the American prairies, where all natural tree cover was eliminated by loss of the riparian areas. Here again, most of the bird species involved are relatively widespread, and/or tolerant of varying habitats, and are unlikely to be seriously threatened by even the more extensive dam–diversion schemes yet proposed.

4. Development

Thus far, I have suggested that few if any bird species are really threatened by development in the boreal forest region, assuming no really drastic changes from patterns of development proposed to date. I have implied that populations of birds of late-climax and riparian communities may be reduced, while those of birds of early succession are likely to increase. These changes seem likely to be much less sweeping than those occasioned by white men settling in the eastern deciduous forest and transition forest regions of northeastern North America, where the combined effect of habitat destruction and unregulated slaughter eliminated two common species (Passenger Pigeon and Carolina Parakeet), at least one subspecies (Heath Hen), and a large number of local populations, besides decimating many others. No doubt there were (partly) compensating — how much is compensation for an extinct species? — increases in species of edge and early successional habitats, and the overall bird density may not have changed very greatly. The boreal forest with its relatively unspecialized bird fauna can be expected to show somewhat parallel, if perhaps less sweeping, changes in response to future development.

Those land birds which were largely or totally eliminated from the eastern states were mostly non-passerines, large enough to be used for food by man, and social or highly gregarious to an extent that breeding seems to have been progressively less successful as their numbers dwindled. Boreal species most commonly suggested as threatened include a few colonial water birds and several raptors. These largely fish-eating birds are involved in food chains concentrating toxic chemicals, rather than being subject to direct exploitation or tied to an environment which is being exploited itself (for purposes other than waste disposal). Other scarce boreal species include other raptors, such as Great Gray Owl, Boreal Owl, and Hawk Owl, which presumably have never existed at other than very low densities, although they range through the boreal zone of Eurasia as well as North America. Their low densities reflect their status as widely dispersed, resident predators, and nothing short of widespread elimination of the northern needle-leafed forests is likely to seriously threaten their continued existence. Scarce, short-lived, migrant passerines are perhaps more vulnerable, but few of these are so restricted in range as to be viewed with alarm. Connecticut Warbler among the forest birds, and Harris' Sparrow and Golden-crowned Sparrow from the subarctic and subalpine ecotones respectively, are relatively scarce and also restricted in range; the last of these, like all mountain species, must have existed as isolated populations on each mountain or range through much of its existence. The impact of development is likely to be felt mainly on a local scale. Overall, the changes are unlikely to be sweeping, unless new enormities as yet undreamed of can be proliferated before shortages of fossil fuels — on which most recent developments both depend and use as justification for their existence — makes them totally impracticable.

5. Pollution

Pollution is one of the ultimate enormities, capable of affecting the entire biosphere. Until recently, the natural environment was believed large enough and tolerant enough to absorb all the wastes man might discard, and where man is limited in numbers, mobility, and in the products and materials at his disposal, this may still be the case. But now with modern technology and mobility, the pollutants turned loose in the environment include many synthetic and persistent toxic chemicals, plus oil and other petroleum fractions, plus fumes that combine with atmospheric moisture to produce acid rain, not to mention the bogey of radioactive nuclear wastes. The loss of Peregrine Falcons from more than half of North America as a result of overuse of chlorinated hydrocarbon poisons in controlling insects is well documented (e.g., Fyfe, Temple, and Cade 1976), as is the widespread impact on fish-eating birds of other insecticides and industrial chemicals, and the end is not in sight. The vested interests of persons concerned with their own short-term economic and political gains still continue to thwart most efforts aimed at ensuring that the natural environment remains a healthy and satisfying place for people — and birds — to live in.

6. Global ecosystem

If we are to learn any ecological lessons from study of boreal birds, they must include the concept that Canadian ecosystems are not isolated. Rather these are a part of at least a hemispheric ecosystem as far as nature goes, and of a global ecosystem as far as man's place and needs are concerned. The boreal region is fascinating, but distinctly limited in its resources. We should try to ensure that the opportunities for fascination are not too severely limited by the extraction of resources, for its capacity for self-regeneration is also limited. Up to the present, its relatively enormous area and inhospitable climate have spared it the sweeping alterations suffered by more accessible ecosystems. In the future, the high energy costs of resource extraction there may help to reduce the rate of exploitation to something nearer what the environment can cope with. But the real decisions will have to be made by people, and the choice of "wilderness" or "desert" is not an idle joke. If the earth can be kept a good place for birds, the survival of mankind is ensured. If not, what?

References

Acres Research and Planning Ltd. 1967. Mid-Canada development corridor... a concept. Lakehead Univ. Thunder Bay, Ont.

Addy, C. E. 1953. Fall migration of the Black Duck. US Dep. Int. Fish and Wildl. Serv. Spec. Sci. Rpt. Wildl. No. 19. 63 pp. 32 fig.

American Birding Association. 1975. ABA Check-list: Birds of continental United States and Canada. Foxx Printers, Austin, Texas. 1st ed. 64 pp.

American Ornithologists' Union. 1957. Check-list of North American birds. 5th ed. AOU. Port City Press Inc., Baltimore, Maryland. 691 pp.

American Ornithologists' Union. 1973. Thirty-second supplement to the AOU Check-list of North American birds. Auk 90:411–419.

American Ornithologists' Union. 1976. Thirty-third supplement to the AOU Check-list of North American birds. Auk 93:875–879.

Baldwin, W. K. W. and members of the excursion. 1962. Report on botanical excursion to the boreal forest region in northern Quebec and Ontario. Spec. Rep., Nat. Mus. Canada. Dep. Nor. Aff. and Natur. Resources.

Bell, B. D., C. K. Catchpole, K. J. Corbett, and R. J. Hornby. 1973. The relationship between census results and breeding populations of some marshland passerines. Bird Study 20:127–140.

Berthold, P. 1976. Methoden der Bestandserfassung in der Ornithologie: Ubersicht und kritische Betrachtung. J. fur Ornithol. 117:1–69.

Best, L. B. 1975. Interpretational errors in the "mapping method" as a census technique. Auk 92:452–460.

Blem, C. R. 1973. Geographic variation in the bioenergetics of the House Sparrow. Ornithol. Monogr. (AOU) No. 14:96–121.

Bock, C. E. and L. W. Lepthien, 1976. Synchronous eruptions of boreal seed-eating birds. Amer. Natur. 110:559–571.

Bourassa, R. 1973. La Baie James. Editions du Jour, Montréal. 139 pp.

Braun, E. L. 1950. Deciduous forests of eastern North America. The Blakiston Co., Philadelphia. 596 pp.

Breckenridge, W. J. 1956. Measurements of the habitat niche of the Least Flycatcher. Wilson Bull. 68:47–51.

Brewer, R. 1967. Bird populations of bogs. Wilson Bull. 79:371–396.

Bryson, R. A. 1966. Air masses, streamlines, and the boreal forest. Geogr. Bull. 8(3):228–269.

Buckner, C. H., A. J. Erskine, R. Lidstone, B. B. McLeod, and M. Ward. 1975. The breeding bird community of coast forest stands on northern Vancouver Island. Murrelet. 56(3):6–11.

Carbyn, L. N. 1971. Densities and biomass relationships of birds nesting in boreal forest habitats. Arctic 24:51–61.

Clark, R. J. 1975. A field study of the Short-eared Owl, *Asio flammeus* (Pontoppidan), in North America. Wildl. Monogr. No. 47. 67 pp.

Conner, R. N. and C. S. Adkisson. 1975. Effects of clearcutting on the diversity of breeding birds. J. Forest. 73:781–786.

Dirschl, H. J. 1972. Evaluation of ecological effects of recent low water levels in the Peace–Athabasca Delta. Can. Wildl. Serv. Occ. Pap. No. 13. 27 pp.

Edwards, Y. 1969. The hardwood forests that vanished. Ont. Natur. 2/69:9–12.

Erskine, A. J. 1957. Weedy pond, spruce–hemlock wood, and second-growth spruce–maple brush. Census 34. Aud. Field Notes. 11:456–457.

Erskine, A. J. 1968*a*. Birds observed in north-central Alberta, summer 1964. Blue Jay. 26:24–31.

Erskine, A. J. 1968*b*. Sedge–sweet gale marsh. Census 53. Aud. Field Notes. 22:702–704.

Erskine, A. J. 1970*ff*. The co-operative Breeding Bird Survey in Canada, 1966–69, 1970, 1971, 1972, 1973, 1974, 1975. Can. Wildl. Serv. Progr. Notes Nos. 15, 21, 26, 32, 38, 45, 60. 19, 33, 29, 15, 15, 19, 15 pp.

Erskine, A. J. 1971*a*. A preliminary catalogue of bird census (plot) studies in Canada, (Part I), Can. Wildl. Serv. Progr. Notes. No. 20. 78 pp.

Erskine, A. J. 1971*b*. Bird communities in and around Cape Breton wetlands. Can. Field-Natur. 85:129–140.

Erskine, A. J. 1971*c*. Some new perspectives on the breeding ecology of Common Grackles. Wilson Bull. 83:352–370.

Erskine, A. J. 1972. A preliminary catalogue of bird census plot studies in Canada, Part 2. Can. Wildl. Serv. Progr. Notes. No. 30. 42 pp.

Erskine, A. J. 1974*a*. Off into the wet green yonder: birds and plants of a boreal bog. Blue Jay. 32:33–37.

Erskine, A. J. 1974*b*. Problems associated with bird populations not adequately sampled by the mapping census method. Acta Ornithol. XIV(24):340–346.

Erskine, A. J. 1974*c*. Mature aspen stand. Census 135. Amer. Birds. 28:1046.

Erskine, A. J. 1974*d*. Balsam poplar bottomland. Census 134. Amer. Birds. 28:1045–1046.

Erskine, A. J. 1976. A preliminary catalogue of bird census plot studies in Canada. Part 3. Can. Wildl. Serv. Progr. Notes. No. 59. 24 pp.

Erskine, A. J. and G. S. Davidson, 1976. Birds in the Fort Nelson lowlands of northeastern British Columbia. Syesis. 9:1–11.

Erskine, A. J. and R. C. Stein, 1964. A re-evaluation of the avifauna of the Cariboo Parklands. B.C. Prov. Mus. Natur. Hist. and Anthropol. Rep. 1963. AA18–AA35.

Ferry, C. and B. Frochot. 1970. L'avifaune nidificatrice d'une forêt de chene pedoncules en Bourgogne: étude de deux successions écologiques. Terre et Vie. 1970:153–250.

Flack, J. A. D. 1976. Bird populations of aspen forests in western North America. Ornithol. Monogr. (AOU) No. 19. 97 pp.

Forestry Branch. 1950. Native trees of Canada. Canada. Dep. Resources and Develop. Bull. 61. 4th Ed. 293 pp.

Fretwell, S. D. 1972. Populations in a seasonal environment. Monogr. Population Biol. No. 5. Princeton Univ. Press, Princeton, N.J. 217 pp.

Fyfe, R., S. A. Temple, and T. J. Cade. 1976. The North American Peregrine survey, 1975. Can. Field-Natur. 90:228–273.

Gillespie, W. L. 1960. Breeding bird and small mammal populations in relation to the forest vegetation of the subarctic region of northern Manitoba. Unpubl. Ph.D. Thesis, Univ. Ill. 120 pp.

Godfrey, W. E. 1966. The birds of Canada. Nat. Mus. Canada Bull. No. 203. 428 pp.

Godfrey, W. E. 1976. Breeding status of the Common Redpoll in Alberta and Saskatchewan. Can. Field-Natur. 90:199–200.

Goulden, L. L. 1974. Mature poplar–spruce island. Census 142. Amer. Birds. 28:1050.

Haapanen, A. 1965. Bird fauna of the Finnish forests in relation to forest succession. I. Ann. Zool. Fennici. 2:153–196.

Haffer, J. 1974. Avian speciation in tropical South America. Publ. Nuttall Ornithol. Club. No. 14. Cambridge, Mass. 390 pp.

Hagar, D. C. 1960. The interrelationships of logging, birds, and timber regeneration in the Douglas-fir region of northwestern California. Ecology. 41:116–125.

Holmes, R. T. and F. W. Sturges. 1973. Annual energy expenditure by the avifauna of a northern hardwoods ecosystem. Oikos. 24:24–29.

Horvath, O. 1963. Contributions to nesting ecology of forest birds. Unpubl. M. For. Thesis. Univ. B.C. 181 pp.

Hubbard, J. P. 1969. The relationships and evolution of the *Dendroica coronata* complex. Auk. 86:393–432.

International Bird Census Committee. 1970. Recommendations for an international standard for a mapping method in bird census work. *In* Bird Census Work and Environmental Monitoring. Bull. Ecol. Res. Comm. No. 9:49–52. (Also *in* Aud. Field Notes. 1970. 24:723–726).

James, F. C. and H. H. Shugart, Jr. 1970. A quantitative method of habitat description. Aud. Field Notes. 24:727–736.

Johansen, H. 1963. Zoogeographical aspects of the birds of the subarctic. Proc. XIII Int. Ornithol. Congr. 1117–1123.

Johnston, D. W. and E. P. Odum. 1956. Breeding bird populations in relation to plant succession on the piedmont of Georgia. Ecology. 37:50–62.

Karr, J. R. 1976. On the relative abundance of migrants from the north temperate zone in tropical habitats. Wilson Bull. 88:433–458.

Kendeigh, S. C. 1946. Breeding birds of the beech–maple–hemlock community. Ecology. 27:226–245.

Kendeigh, S. C. 1947. Bird population studies in the coniferous forest biome during a spruce budworm outbreak. Ont. Dep. Lands and Forests. Biol. Bull. 1:1–100.

Kendeigh, S. C. 1948. Bird populations and biotic communities in southern lower Michigan. Ecology. 29:101–114.

Lamb, H. H. 1975. Our understanding of the global wind circulation and climatic variations. Bird Study. 22:121–141.

LaRoi, G. H. 1967. Ecological studies in the boreal spruce–fir forests of the North American taiga. I. Analysis of the vascular flora. Ecol. Monogr. 37:229–253.

Lincoln, F. C. 1950. Migration of birds. US Dep. Int. Fish and Wildl. Serv. Cir. No. 16, 102 pp.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology. 39:599–619.

MacArthur, R. H. 1959. On the breeding distribution pattern of North American migrant birds. Auk. 76:318–325.

MacArthur, R. H. and J. W. MacArthur. 1961. On bird species diversity. Ecology. 42:353–357.

MacDonald, J. E. 1965. A bird census in red pine plantations and mixed stands in Kirkwood Township, Ontario. Can. Field-Natur. 79:21–25.

Maher, W. J. 1970. Birds. *In* Matador Project. 3rd Annu. Rep. Can. Comm. IBP. Saskatoon, Sask. Pages 81–149, 278–286.

Martin, N. D. 1960. An analysis of bird populations in relation to forest succession in Algonquin Provincial Park, Ontario. Ecology. 41:126–140.

Mengel, R. M. 1964. The probable history of species formation in some northern wood warblers (Parulidae). Living Bird. 3:9–43.

Merriam, C. H. 1894. The geographic distribution of animals and plants in North America. US. Dep. Agr. Yearbook, Washington, D.C. Pages 203–214.

Millar, J. B. 1976. Wetland classification in western Canada: A guide to marshes and shallow water wetlands in the grasslands and parklands of the Prairie Provinces. Can. Wildl. Serv. Rep. Ser. No. 37. 37 pp.

Moreau, R. E. 1966. The bird faunas of Africa and its islands. Acad. Press, New York and London. 424 pp.

Morris, R. F., W. F. Cheshire, C. A. Miller, and D. G. Mott. 1958. The numerical response of avian and mammalian predators during a gradation of the spruce budworm. Ecology. 39:487–494.

Munroe, E. 1956. Canada as an environment for insect life. Can. Entomol. 88:372–476.

Newton, I. 1972. Finches. New Natur. No. 55. Collins, London. 288 pp.

Oelke, H. 1966. 35 years of breeding-bird census work in Europe. Aud. Field Notes. 20:635–642.

Oelke, H. 1968. Wo beginnt bzw. wo endet der Biotop der Feldlerche? J. fur Ornithol. 109:25–29.

Robbins, C. S. and W. T. Van Velzen. 1967. The breeding bird survey, 1966. US. Dep. Int. Fish and Wildl. Serv. Spec. Sci. Rep. No. 102. 43 pp.

Robbins, C. S. and W. T. Van Velzen. 1969. The breeding bird survey, 1967 and 1968. US. Dep. Int. Fish and Wildl. Serv. Spec. Sci. Rep. No. 124. 107 pp.

Rowe, J. S. 1959. Forest regions of Canada. Canada. Dep. North. Aff. Nat. Resources. Forest. Br. Bull. 123. 71 pp.

Short, L. L., Jr. 1965. Hybridization in the flickers (*Colaptes*) of North America. Bull. Amer. Mus. Natur. Hist. 129:307–428.

Short, L. L., Jr. 1967. A review of the genera of grouse (Aves, Tetraonidae). Amer. Mus. Novit. No. 2289. 39 pp.

Short, L. L. 1974. Habits and interactions of North American three-toed woodpeckers (*Picoides arcticus* and *Picoides tridactylus*). Amer. Mus. Novit. No. 2547. 42 pp.

Sjörs, H. 1963. Amphi-Atlantic zonation, nemoral to arctic. *In* North Atlantic biota and their history. A. Löve and D. Löve, eds. Symp. Publ. Div. Pergamon Press, Oxford. Pages 109–125.

Smith, S. M. 1967. An ecological study of winter flocks of Black-capped and Chestnut-backed Chickadees. Wilson Bull. 79:200–207.

Snyder, D. P. 1950. Bird communities in the coniferous forest biome. Condor. 52:17–27.

Stein, R. C. 1963. Isolating mechanisms between populations of Traill's Flycatchers. Proc. Amer. Phil. Soc. 107:21–50.

Stewart, R. E., and J. W. Aldrich. 1952. Ecological studies of breeding bird populations in northern Maine. Ecology. 33:226–238.

Sturman, W. A. 1968. The foraging ecology of *Parus atricapillus* and *P. rufescens* in the breeding season, with comparisons with other species of *Parus*. Condor. 70:309–322.

Svensson, S. 1974. Interpersonal variation in species map evaluation in bird census work with the mapping method. Acta Ornith. XIV(23):323–338.

Theberge, J. B. 1976. Bird populations in the Kluane Mountains, southwest Yukon, with special reference to vegetation and fire. Can. J. Zool. 54:1346–1356.

Tisdale, E. W. and A. McLean. 1957. The Douglas-fir zone of southern British Columbia. Ecol. Monogr. 27:247–266.

Tramer, E. J. 1974. Proportions of wintering North American birds in disturbed and undisturbed dry tropical habitats. Condor. 76:460–464.

Tufts, R. W. 1962. The birds of Nova Scotia. Nova Scotia Museum, Halifax. 481 pp.

Udvardy, M. D. F. 1963. Bird faunas of North America. Proc. XIII Int. Ornithol. Congr. Pages 1147–1167.

Vermeer, K. 1973. Some aspects of the breeding and mortality of Common Loons in east-central Alberta. Can. Field-Natur. 87:403–408.

Webster, J. D. and D. L. Adams. 1973. Breeding bird censuses in old-growth deciduous forests. Ind. Acad. Sci. Proc. for 1972. 82:198–206.

Whitfield, D. W. A., J. M. Gerrard, W. J. Maher, and D. W. Davis. 1974. Bald Eagle nesting habitat, density, and reproduction in central Saskatchewan and Manitoba. Can. Field-Natur. 88:399–407.

Williams, A. B. 1936. The composition and dynamics of a beech–maple climax community. Ecol. Monogr. 6:317–408.

Appendices

Appendix 1
Supplementary references for Tables 3, 5–10, 12
The name of the compiler is always given first, regardless of the order in the published version; when three or more "authors" are given in the published version, this is shown here as "Compiler *et al.*", regardless of the original order of names. Those references marked ( ) are already in the main reference list.

I. Progress Note no. 20

(17) Erskine, A. J. 1968*a*. Sedge–sweet gale marsh. Aud. Field Notes. 22:702–704.

18 Erskine, A. J. 1968*b*. Spruce bog. Aud. Field Notes. 22:704–705.

20 Erskine, A. J. 1969*a*. Poplar–birch forest. Aud. Field Notes. 23:702–703.

21 Erskine, A. J. 1969*b*. Fir–spruce forest. Aud. Field Notes. 23:714–716.

23 Erskine, A. J. 1969*d*. Jack pine forest. Aud. Field Notes. 23:713–714.

24 Erskine, A. J. 1969*e*. Spruce bog. Aud. Field Notes. 23:739–740.

25 Fairfield, G. M. 1959. Tamarack swamp. Aud. Field Notes. 13:463–464.

(41) Gillespie, W. L. 1960. Breeding bird and small mammal populations in relation to the forest vegetation of the subarctic region of northern Manitoba. Unpubl. Ph. D. Thesis. Dep. Zool., Univ. Ill. 121 pp.

47 Goodwin, C. E. and J. Jarvis. 1964. Tamarack swamp. Aud. Field Notes. 18:551–552.

49 Grant, J. 1965. Mature coniferous forest. Aud. Field Notes. 19:596–598.

50 Grant, J. 1966. Northern subalpine forest. Aud. Field Notes. 20:630–631.

(57) Kendeigh, S. C. 1947. Bird population studies in the coniferous forest biome during a spruce budworm outbreak. Ont. Dep. Lands and Forests. Biol. Bull., 1:1–100.

(65) Martin, N. D. 1960. An analysis of bird populations in relation to forest succession in Algonquin Provincial Park, Ont. Ecology. 41:126–140.

69 McNeil, R. 1964. Territorialité, densité et diversité des communautés chez certains Passèriformes de la Province de Québec. Thèse de maîtrise ès Sciences. Inédite. Dép. de Zool. Univ. de Montréal.

72 Mook, L. J. A 20-year bird census in a spruce–fir habitat. Unpubl. draft ms.

75 Oelke, H. 1967*a*. Mature pine stand (85–95 years old) of the southern Canadian Shield. Aud. Field Notes. 21:617.

76 Oelke, H. 1967*b*. Mature pine stand (100–110 years old) of the southern Canadian Shield. Aud. Field Notes. 21:617–618.

94 Speirs, J. M. 1949. The relation of DDT spraying to the vertebrate life of the forest. *In* Forest spraying and some effects of DDT. Ont. Dep. Lands and Forests. Biol. Bull. 2:141–158.

100 Stewart, R. E. 1955*a*. Virgin bottomland white spruce forest. Aud. Field Notes. 9:415–416.

101 Stewart, R. E. 1955*b*. Virgin upland white spruce forest. Aud. Field Notes. 9:416.

104 Webster, J. D. 1969*a*. White spruce forest. Aud. Field Notes. 23:717.

115 Sanders, C. J. 1970. Populations of breeding birds in the spruce–fir forests of northwestern Ontario. Can. Field-Natur. 84:131–135.

II. Progress Note no. 30

(8) Carbyn, L. N. 1971. Densities and biomass relationships of birds nesting in boreal forest habitats. Arctic. 24:51–61.

118 Erskine, A. J. 1970*a*. Mature poplar forest. Aud. Field Notes. 24:742–743.

119 Erskine, A. J. 1970*b*. Mixed jack pine forest. Aud. Field Notes, . 24:751–752.

120 Erskine, A. J. 1970*c*. Disturbed fir – spruce forest with alder openings. Aud. Field Notes 24:752–753.

121 Erskine, A. J. 1970*d*. Black spruce forest. Aud. Field Notes. 24:753–754.

122 Erskine, A. J. 1970*e*. Tamarack bog. Aud. Field Notes. 24:768–769.

123 Erskine, A. J. 1970*f*. Black spruce bog. Aud. Field Notes. 24:769–771.

124 Erskine, A. J. 1970*g*. Urban area — commercial and residential. Aud. Field Notes. 24:774–775.

125 Erskine, A. J. 1971*a*. Mature poplar forest. Amer. Birds. 25:977–978.

126 Erskine, A. J. 1971*b*. Black spruce forest. Amer. Birds. 25:985–986.

127 Erskine, A. J. 1971*c*. Mature jack pine forest. Amer. Birds. 25:986–987.

128 Erskine, A. J. 1971*d*. Disturbed fir–spruce forest with alder openings. Amer. Birds. 25:991.

133 Hope, C. E. 1945. Bird population studies in Algonquin Park, 1945. Unpubl. typed rep. (copy in CWS files). Res. Div., Ont. Dep. Lands and Forests, Maple. 23 pp.

134 Hope, C. E. 1946. Bird population studies in Algonquin Park, 1946. Unpubl. typed rep. (copy in CWS files). Res. Div. Ont. Dep. Lands and Forests, Maple. Pages 30–43.

143 Sergeant, D. E. and I. A. McLaren. Unpubl. Sum. (copy in CWS files).

150 Speirs, J. M. *et al.* 1971*b*. Leatherleaf bog. Amer. Birds. 25:1005–1006.

154 Whitelaw, C. J. 1953. Ecological studies of breeding bird populations in Algonquin Provincial Park. Unpubl. B. A. Thesis. Dep. Biol., Queen's Univ., Kingston. 47 pp.

155 Wilson, W. G. 1968. Habitat selection of forest birds in central New Brunswick. Unpubl. M.Sc. Thesis. Dep. Biol., York Univ., Toronto.

III. Progress Note no. 59

157 Banville, D. 1973. Inventaire d'oiseaux nicheurs à la réserve nationale du Cap Tourmente. (Unpubl. typed rep. in CWS files).

159 Buckner, C. H. and W. J. Turnock. 1965. Avian predation on the larch sawfly, *Pristiphora erichsonii* (Htg.), (Hymenoptera; Tenthredinidae). Ecology. 46:223–236 (bird data re-interpreted by A.J.E.; copy in CWS files).

161 Chemical Control Research Institute, Environment Canada. Unpubl. data from work in Ont. and Man. (bird data re-interpreted by A.J.E.; copy in CWS files).

162 Cyr, A. 1974. L'avifaune nicheuse de deux types d'associations forestières dans la zone du nouvel aéroport international à Mirabel, Québec. Mem. de Maîtrise es Sciences. Inédit. Dep. de Biol. Univ. de Montréal, 237 pp.

163 DesGranges, J.-L. 1973. Inventaires ornithologiques au Park National de La Mauricie, Québec. Dossier No. 36/5R2, 9 avifaune, Phase II. Parks Canada. Unpubl. rep. (copy in CWS files).

165 Erskine, A. J. 1972*a*. Mature poplar stand. Amer. Birds. 26:989–990.

166 Erskine, A. J. 1972*b*. Black spruce stand. Amer. Birds. 26:990.

167 Erskine, A. J. 1972*c*. Jack pine stand. Amer. Birds. 26:990–991.

168 Erskine, A. J. 1972*d*. Balsam fir stand. Amer. Birds. 26:991–992.

169 Erskine, A. J. 1972*e*. Shrubby marsh. Amer. Birds. 26:992–993.

170 Erskine, A. J. 1972*f*. Urban area, commercial and residential. Amer. Birds. 26:1000.

171 Erskine, A. J. 1973*a*. Mature birch and poplar forest. Amer. Birds. 27:1007.

172 Erskine, A. J. 1973*b*. Young aspen forest. Amer. Birds. 27:1007–1008.

173 Erskine, A. J. 1973*c*. Balsam fir forest. Amer. Birds. 27:1009–1010.

174 Erskine, A. J. 1973*d*. Black spruce stand with alder swales. Amer. Birds. 27:1010.

(175) Erskine, A. J. 1974*a*. Off into the wet green yonder: birds and plants of a boreal bog. Blue Jay. 32:33–37.

(176) Erskine, A. J. 1974*b*. Balsam poplar bottomland. Amer. Birds. 28:1045–1046.

(177) Erskine, A. J. 1974*c*. Mature aspen stand. Amer. Birds. 28:1046.

178 Erskine, A. J. 1974*d*. Black spruce stand on mountainside. Amer. Birds. 28:1047.

179 Erskine, A. J. 1974*e*. Bottomland white spruce forest. Amer. Birds. 28:1047–1948.

180 Erskine, A. J. 1974*f*. Stunted black spruce on raised bog. Amer. Birds. 28:1048.

181 Erskine, A. J. 1974*g*. Small town residential area with wooded vacant lots. Amer. Birds. 28:1053–1054.

(190) Goulden, L. L. 1974*c*. Mature poplar–spruce island. Amer. Birds. 28:1050.

191 Harris, W. C. *et al.* 1974. Upland lichen woodland. Amer. Birds. 28:1048–1049.

195 Lamberton, R. D. 1975. Avifaunal survey of Gros Morne National Park: preliminary report. Parks Canada contract 74–46. Appendix no. 1. Pages 80–86.

196 Lunn, S. Avifaunal survey of Kejimkujik National Park: preliminary report. Parks Canada contract.

200 McLeod, J. M. 1974. Bird populations studies in the Swaine jack pine sawfly life system. Centre de recherches forestières des Laurentides. Rapp. Inf. LAU-X-10. 86 pp.

218 Tull, C. E. 1973. White cedar–balsam fir swamp forest. Amer. Birds. 27:1008–1009.

219 Tull, C. E. *et al.* 1973. Open sphagnum bog. Amer. Birds. 27:1010–1011.

221 Erskine, A. J. 1975*a*. Aspen–willow forest. Amer. Birds. 29:1131–1132.

222 Erskine, A. J. 1975*b*. Black cottonwood floodplain forest. Amer. Birds. 29:1132–1133.

223 Erskine, A. J. 1975*c*. Disturbed white spruce stand with willow swales. Amer. Birds. 29:1137–1138.

224 Erskine, A. J. 1975*d*. Subalpine conifer forest. Amer. Birds. 29:1133–1134.

225 Erskine, A. J. 1975*e*. Lodgepole pine forest. Amer. Birds. 29:1134–1135.

226 Erskine, A. J. 1975*f*. Urban area, commercial and residential. Amer. Birds. 29:1145.

228 Speirs, J. M., and R. Orenstein. 1975. Bird populations in forests of Ontario County, 1966–1968. Ont. Field Biol. 29:1–24.

IV. Other

Ebel, G.R.A., *et al.* 1975. Black Spruce Scrub–Muskeg. Amer. Birds. 29:1136–1137.

Erskine, A. J. 1977. Urban residential. Amer. Birds. 31:90–91.

Gage, S. H. Unpubl. sum. based on data from Can. Forest. Serv. files (copy in CWS file) — supplementing data given by Mook (I:72).

V. Additional references for census plots summarized in Table 7

Not in Progress Notes (data for USA plots)

Archie, M. A. and R. A. Hudson. 1973. Scattered mixed coniferous forest in subalpine meadows and spruce bogs. Amer. Birds. 27:1002–1003.

Burr, R. M. 1969*a*. Englemann's Spruce–Alpine Fir forest. Aud. Field Notes. 23:755–756.

Burr, R. M. 1969*b*. Logged Englemann's Spruce–Alpine Fir forest. Aud. Field Notes. 23:756.

Frissell, S. S. 1973. Disturbed Douglas fir–lodgepole pine forest. Amer. Birds. 27:1001.

Hering, L. 1948. Nesting birds of the Black Forest, Colorado. Condor. 50:49–56.

Hering, L. 1956. Lower foothills, ponderosa pine forest. Aud. Field Notes. 10:423.

Hering, L. 1958. Open ponderosa pine forest. Aud. Field Notes. 12:448.

Longley, W. H. 1944. Northern forest. Aud. Magazine. sect. II. 24.

Manuwal, D. A. 1967*a*. Ponderosa pine – Douglas fir montane forest. Aud. Field Notes. 21:623–624.

Manuwal, D. A. 1967*b*. Lodgepole–larch–Douglas fir montane forest. Aud. Field Notes. 21:624–626.

Robert H. 1966. Red fir–lodgepole pine forest. Aud. Field Notes. 20:625–626.

( ) Snyder, D. P. 1950. Bird communities in the coniferous forest biome. Condor. 52:17–27.

Thatcher, D. M. 1955*a*. Immature lodgepole pine forest. Aud. Field Notes. 9:417.

Thatcher, D. M. 1955*b*. Immature Douglas fir forest. Aud. Field Notes. 9:418–419.

Thatcher, D. M. 1956. Upper foothills, ponderosa pine forest. Aud. Field Notes. 10:421–423.

Webster, J. D. 1967. Lodgepole pine–spruce forest. Aud. Field Notes. 21:622.

Appendix 2
Tree Summaries

1. Spruce plots

Plot	No. trees /acre	Basal area (ft^2/ac.)	≥6 in.;	% of trees 12 in.	Mean canopy ht. (ft)	Canopy cover (%)	Ground cover (%)	Shrub stems /acre	Major tree species with % age density, dominance, frequency	
Doaktown, N.B.	218*	70.3	52;	7	46	ca. 50	ca. 75	313+	Red Spruce	40, 42, 98
									Red/Sugar Maple	22, 10, 96
									Balsam Fir	14, 8, 86
									White Pine	11, 29, 71
									Paper Birch	11, 9, 63
Pascalis, Que.	155*	38.1	6;	0	26	29	ca. 95	426+	Black Spruce	89, 89, 100
									Balsam Fir	6, 6, 19
Ghost River, Ont.	267*	46.1	31;	0	47	36	ca. 95	680+	Black Spruce	93, 94, 100
									Balsam Fir	6, 4, 25
Mafeking, Man.	842	125.0	7;	0	36	55	98	1049	Black Spruce	97, 98, 100
Dore Lake, Sask.	647	112.8	14;	2	47	53	80	1340	Black Spruce	84, 61, 78
									White Spruce	8, 28, 36
									Trembling Aspen	4, 6, 21
Kledo Creek, B.C.	603	195.4	55;	8	80	59	84	255	White Spruce	78, 78, 100
									Black Spruce	6, 4, 60
									Trembling Aspen	9, 12, 60
Steamboat, B.C.	458	136.2	49;	4	72	57	80	1128	Black Spruce	75, 65, 100
									White Spruce	5, 10, 50
									Paper Birch	9, 10, 54
Round Lake, B.C.	341*	106.2	53;	6	68	42	71	3170	White Spruce	74, 79, 100
									Trembling Aspen	20, 15, 95

* Disturbed areas.

2. Fir plots

Plot	No. trees /acre	Basal area (ft^2/ac.)	≥6 in.;	% of trees 12 in.	Mean canopy ht. (ft)	Canopy cover (%)	Ground cover (%)	Shrub stems /acre	Major tree species with % age density, dominance, frequency	
Foreston, N.B.	385*	79.8	44;	0	40	ca. 60	ca. 65	932+	Balsam Fir	69, 67, 96
									Red Spruce	22, 22, 50
									Paper Birch	8, 9, 75
Lac Dances, Que.	219*	66.4	48;	5	47	ca. 45	ca. 75	1780	Balsam Fir	64, 52, 93
									Black Spruce	19, 22, 82
									Balsam Poplar	5, 8, 14
Steeprock Bay, Man.	298*	126.8	27;	1	42	64	ca. 65	1657	Balsam Fir	40, 43, 100
									White Spruce	6, 10, 95
									Trembling Aspen	30, 16, 60
									Paper Birch	20, 25, 95
Sled Lake, Sask.	372	95.3	26;	7	61	72	54	1844	Balsam Fir	75, 57, 100
									White Spruce	6, 11, 95
									Trembling Aspen	10, 12, 65
									Balsam Poplar	4, 11, 55
									Paper Birch	4, 8, 80

cont'd. on page 66

2. Fir plots *cont'd.*

Plot	No. trees /acre	Basal area (ft^2/ac.)	% of trees ≥6 in.; 12 in.	Mean canopy ht. (ft)	Canopy cover (%)	Ground cover (%)	Shrub stems /acre	Major tree species with % age density, dominance, frequency	
Astlais Mtn., B.C.	467	158.2	58; 8	63	54	81	603	Subalpine Fir	46, 37, 94
								Englemann Spruce	37, 44, 100
								Lodgepole Pine	16, 18, 56

* Disturbed areas.

3. Pine plots

Plot	No. trees /acre	Basal area (ft^2/ac.)	% of trees ≥6 in.; 12 in.	Mean canopy ht. (ft)	Canopy cover (%)	Ground cover (%)	Shrub stems /acre	Major tree species with % age density, dominance, frequency	
Renous, N.B.	381	48.6	18; 0	32	ca. 20	ca. 20	335	Jack Pine	93, 92, 100
								Black Spruce	7, 8, 90
Belcourt, Que.	198	45.3	29; 1	36	ca. 25	ca. 40	1119	Jack Pine	67, 77, 98
								Black Spruce	13, 10, 75
								Trembling Aspen	16, 10, 60
Matheson, Ont.	238	62.1	51; 0	41	ca. 20	ca. 50	644	Jack Pine	94, 96, 100
								Trembling Aspen	4, 3, 11
Bellsite, Man.	256	46.7	24; 0	27	42	ca. 95	502	Jack Pine	97, 98, 100
Telkwa, B.C.	446	79.6	32; 0	54	30	60	315	Lodgepole Pine	100, 100, 100

4. Poplar and birch plots

Plot	No. trees /acre	Basal area (ft^2/ac.)	% of trees ≥6 in.; 12 in.	Mean canopy ht. (ft)	Canopy cover (%)	Ground cover (%)	Shrub stems /acre	Major tree species with % age density, dominance, frequency	
Bristol, N.B.	379*	58.2	18; 0	38	ca. 70	ca. 60	1220	Trembling Aspen	50, 51, 95
								Paper Birch	17, 16, 56
								Balsam Fir	19, 17, 61
								White Spruce	8, 11, 67
Garrison Ck., Ont.	367	99.1	49; 3	60	ca. 75	ca. 50	1300	Balsam Poplar	47, 48, 63
								Trembling Aspen	31, 41, 85
								Beaked Willow	9, 5, 78
								Balsam Fir	8, 4, 44
Novra, Man.	307	98.7	52; 3	57	75	ca. 40	9200	Balsam Poplar	52, 62, 83
								Trembling Aspen	27, 26, 58
								Paper Birch	12, 8, 29
Mirasty L., Sask.	230	26.7	18; 0	34	71	63	2210	Trembling Aspen	88, 88, 100
								Balsam Poplar	8, 8, 48
								Paper Birch	3, 3, 29
Michel Pt., Sask.	479	147.9	59; 5	70	80	82	700	Paper Birch	46, 46, 95
								White Spruce	24, 22, 90
								Trembling Aspen	15, 22, 75
								Balsam Poplar	13, 10, 70

cont'd. on page 67

4. Poplar and birch plots *cont'd.*

Plot	No. trees /acre	Basal area (ft^2/ac.)	% of trees ≥ 6 in.; 12 in.	Mean canopy ht. (ft)	Canopy cover (%)	Ground cover (%)	Shrub stems /acre	Major tree species with % age density, dominance, frequency	
Mile 320, A.H. B.C.	302	146.3	54; 13	82	75	67	1285	Trembling Aspen	94, 94, 100
								White Spruce	4, 5, 53
Muskwa River, B.C. (old)	279	166.7	62; 29	85	77	48	920	Balsam Poplar	45, 72, 92
								White Spruce	28, 23, 77
								Mountain Alder	27, 5, 69
(young)	270	74.3	40; 6	41	57	34	1980	Balsam Poplar	97, 99, 100
Telkwa, B.C.	237	170.5	64; 23	84	57	58	7850	Black Cottonwood	43, 72, 100
								Trembling Aspen	28, 14, 45
								Mountain Alder	14, 2, 82
								White Spruce	5, 6, 41
Glentanna, B.C.	482	85.8	29; 0	53	62	85	10000	Trembling Aspen	68, 72, 100
								Willow (sp. ?)	28, 23, 95

* Disturbed area.

Appendix 3

Lists of boreal land birds wintering south of latitude 30°N

1. Species wintering almost entirely in South America

Upland Sandpiper, Black-billed Cuckoo, Common Nighthawk, Eastern Kingbird, Olive-sided Flycatcher, Bank Swallow, Cliff Swallow, Purple Martin, Veery, Red-eyed Vireo, Blackpoll Warbler, Connecticut Warbler, and Canada Warbler.

2. Species wintering entirely in Central America, the West Indies, and Mexico

Vaux's Swift, Rufous Hummingbird, Least Flycatcher, Warbling Vireo, Nashville Warbler, Magnolia Warbler, Cape May Warbler, Black-throated Blue Warbler, Chestnut-sided Warbler, MacGillivray's Warbler, Wilson's Warbler, and Western Tanager.

3. Species wintering entirely in areas south of the continental USA — those listed above, plus the following:

Broad-winged Hawk, Black Swift, Great Crested Flycatcher, Willow Flycatcher, Alder Flycatcher, Eastern Wood Pewee, Western Wood Pewee, Barn Swallow, Swainson's Thrush, Gray-cheeked Thrush, Philadelphia Vireo, Tennessee Warbler, Yellow Warbler, Blackburnian Warbler, Bay-breasted Warbler, Northern Waterthrush, Mourning Warbler, American Redstart, Baltimore Oriole, Rose-breasted Grosbeak.

4. Species wintering entirely in the southernmost USA (areas including parts of Arizona, New Mexico, Texas, Louisiana, Mississippi, Alabama, and all of Florida) and areas farther south — those listed above, plus the following:

Ruby-throated Hummingbird, Hammond's Flycatcher, Dusky Flycatcher, Black-and-White Warbler, Parula Warbler, Black-throated Green Warbler, Ovenbird, Sharp-tailed Sparrow, Clay-coloured Sparrow.

Appendix 4
Scientific names of birds and other organisms named in text, and index*

1. Birds
The order follows AOU Check-list (1957):

Common Loon, *Gavia immer*, 43, 47
Red-necked Grebe, *Podiceps grisegena*, 43
Horned Grebe, *P. auritus*, 43
Eared Grebe, *P. nigricollis*, 43
Western Grebe, *Aechmophorus accidentalis*, 43
Pied-billed Grebe, *Podilymbus podiceps*, 43
White Pelican, *Pelecanus erythrorhynchos*, 45
Double-crested Cormorant, *Phalacrocorax auritus*, 45
Great Blue Heron, *Ardea herodias*, 45, 52
American Bittern, *Botaurus lentiginosus*, 43
Canada Goose, *Branta canadensis*, 40
Mallard, *Anas platyrhynchos*, 43; **11, 13**
Black Duck, *A. rubripes*, 43, 45, 55; **11, 13**
Gadwall, *A. strepera*, 43
Pintail, *A. acuta*, 43
American Wigeon, *A. americana*, 43
Green-winged Teal, *A. crecca*, 43
Blue-winged Teal, *A. discors*, 43
Northern Shoveler, *A. clypeata*, 43
Wood Duck, *Aix sponsa*, 47
Redhead, *Aythya americana*, 43
Ring-necked Duck, *A. collaris*, 43, 45
Canvasback, *A. valisineria*, 43
Greater Scaup, *A. marila*, 43, 55
Lesser Scaup, *A. affinis*, 43, 55
Common Goldeneye, *Bucephala clangula*, 43, 47; **13**
Barrow's Goldeneye, *B. islandica*, 43, 47; **13**
Bufflehead, *B. albeola*, 43
White-winged Scoter, *Melanitta deglandi*, 43
Surf Scoter, *M. perspicillata*, 43
Ruddy Duck, *Oxyura jamaicensis*, 43
Hooded Merganser, *Lophodytes cucullatus*, 47
Common Merganser, *Mergus merganser*, 45, 47
Red-breasted Merganser, *M. serrator*, 45
Goshawk, *Accipiter gentilis*, 31, 55, 56
Sharp-shinned Hawk, *A. striatus*, 38
Red-tailed Hawk, *Buteo jamaicensis*, 31, 38, 52, 56; **13**
Harlan's Hawk, *B. jamaicensis harlani*, **13**
Broad-winged Hawk, *B. platypterus*, 38, 67
Golden Eagle, *Aquila chrysaetos*, 56

*Light numbers are page numbers; bold numbers are table numbers.

Bald Eagle, *Haliaeetus leucocephalus*, 45, 47
Marsh Hawk, *Circus cyaneus*, 43
Osprey, *Pandion haliaetus*, 45
Gyrfalcon, *Falco rusticolus*, 56
Peregrine Falcon, *F. peregrinus*, 59
Merlin, *F. columbarius*, 31
American Kestrel, *F. sparverius*, 41, 42, 49
Capercaillie, *Tetrao tetrix*, **15**
Black Grouse, *T. urogallus*, **15**
Blue Grouse, *Dendragapus obscurus*, 54; **15**
Spruce Grouse, *Canachites canadensis*, 18, 23, 54, 55; **3, 6, 7, 15**
Ruffed Grouse, *Bonasa umbellus*, 23, 35, 52, 55; **5, 6, 8, 9**
Willow Ptarmigan, *Lagopus lagopus*, 42, 56
Heath Hen, *Tympanuchus cupido cupido*, 59
Sharp-tailed Grouse, *Pedioecetes phasianellus*, 40, 42, 56; **14**
Sandhill Crane, *Grus canadensis*, 43
Virginia Rail, *Rallus limicola*, 43
Sora, *Porzana carolina*, 43
Yellow Rail, *Coturnicops noveboracencis*, 43
American Coot, *Fulica americana*, 43
Killdeer, *Charadrius vociferus*, 40, 49
American Woodcock, *Philohela minor*, 45
Common Snipe, *Capella gallinago*, 43, 45; **11**
Upland Sandpiper, *Bartramia longicauda*, 40, 67
Spotted Sandpiper, *Actitis macularia*, 45
Solitary Sandpiper, *Tringa solitaria*, 43, 45
Greater Yellowlegs, *T. melanoleuca*, 43, 45; **13**
Lesser Yellowlegs, *T. flavipes*, 43, 45; **11, 13**
Least Sandpiper, *Calidris minutilla*, 45
Short-billed Dowitcher, *Limnodromus griseus*, 45
Wilson's Phalarope, *Steganopus tricolor*, 43
Herring Gull, *Larus argentatus*, 45
California Gull, *L. californicus*, 45
Ring-billed Gull, *L. delawarensis*, 45
Mew Gull, *L. canus*, 45
Franklin's Gull, *L. pipixcan*, 43
Bonaparte's Gull, *L. philadelphia*, 45
Common Tern, *Sterna hirundo*, 45
Arctic Tern, *S. paradisaea*, 45
Caspian Tern, *S. caspia*, 45
Black Tern, *Chlidonias niger*, 43
Rock Dove, *Columba livia*, 50, 55; **12**
Passenger Pigeon, *Ectopistes migratorius*, 59
Carolina Parakeet, *Conuropsis carolinensis*, 59
Black-billed Cuckoo, *Coccyzus erythrophthalmus*, 67
Great Horned Owl, *Bubo virginianus*, 38

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