edited by
Ludwig N. Carbyn

Wolves in Canada and Alaska

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Wolves in Canada and Alaska: their status, biology, and management

Edited by Ludwig N. Carbyn*

Proceedings of the Wolf Symposium held in Edmonton, Alberta, 12–14 May, 1981

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Cover: Male timber wolf feeding on a prey carcass in the boreal forest (photo: Scot Stewart)

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Photo: Scot Stewart

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Introduction

Ludwig N. Carbyn

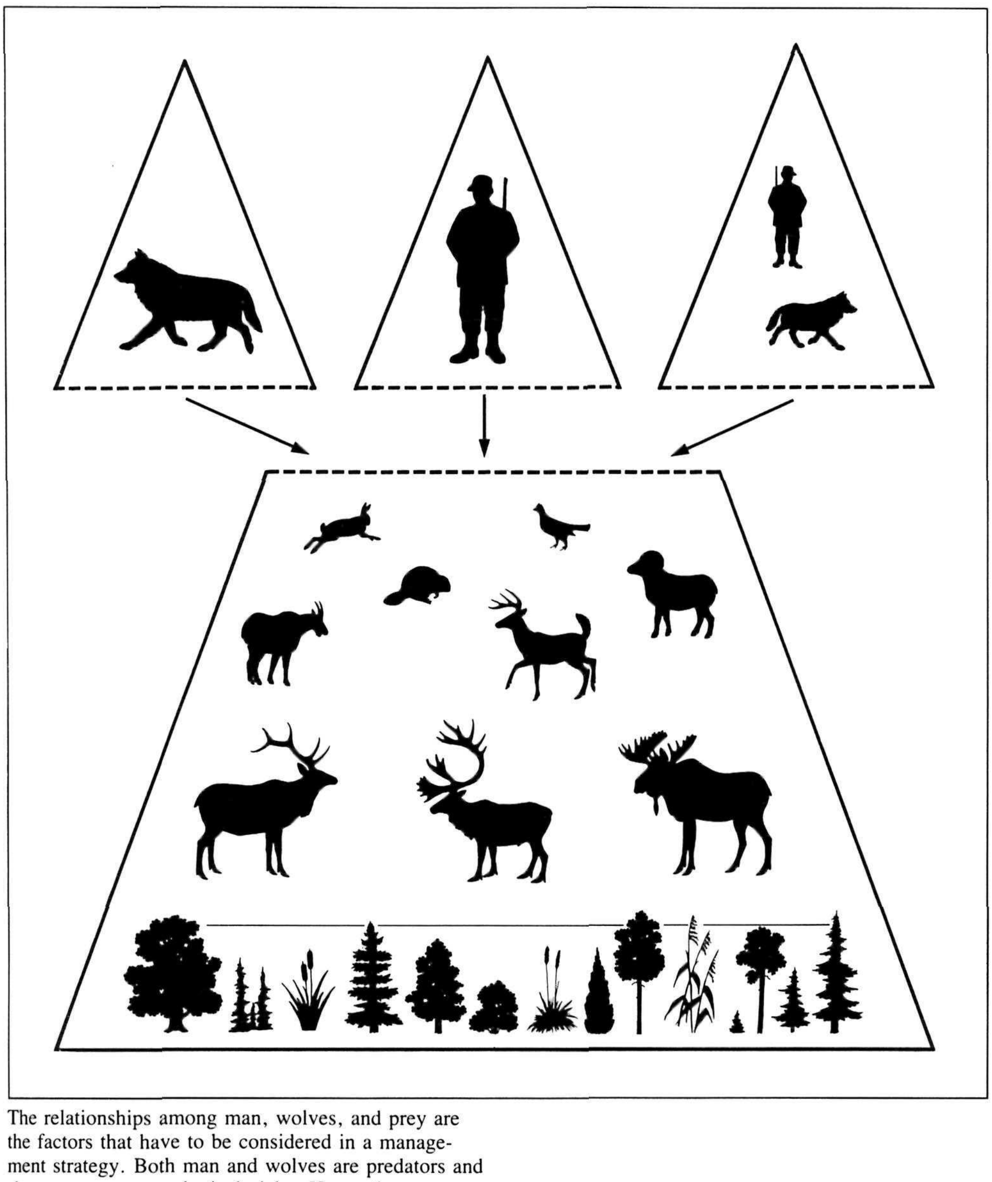
Radio-collared wolf pack (note collar on wolf in centre) travelling through Wood Buffalo National Park in winter (photo: L.N. Carbyn)

The wolf is one of the most controversial wildlife species. Many rural residents and hunters demand its control in areas used for livestock production or where it competes with man for game. Conversely, conservationists (environmentalists, hunters, naturalists), and society in general tend to view the species as a symbol of man's stewardship of wilderness areas. Judging from heated debates and lawsuits on the subject (see Harbo and Dean, this publication), it appears that opposing views in North America are often irreconcilable. In Europe and large parts of Asia the conflict was often resolved by exterminating the species. Recognizing the problems to be faced in preserving wolves in a modern world, Ian McTaggart-Cowan referred to the subject as "a complex and important facet of conservation". In the early 1960s a noted zoologist, the late Douglas Pimlott, asked the probing question "Will the species still exist when the 20th century passes into history? The wolf poses one of the most important conservation questions of our time." John Theberge, in the early 1970s, believed that positive answers to Pimlott's question were emerging, but he cautioned that the future of the wolf depends on public attitudes toward the species. To better understand the present situation in Canada, and in order to make predictions (nebulous as they may be) it is worthwhile examining events of the immediate past and placing the current status of the wolf within an historical perspective.

Indiscriminate large-scale programs of wolf control were widespread over North America in the first half of the 20th century. This led to the extirpation of the species from some areas and its near extinction in others. Remnant populations remained in remote, particularly northern, areas. Within the last 20–40 years a greater measure of protection for the species came about as a consequence of increasingly vocal pro-wolf sentiments expressed by a predominantly non-rural public. People with urban lifestyles, many of whom have neither seen nor heard wolves, wanted the species to remain as part of their wildlife heritage. Increasingly protective legislation was passed to outlaw indiscriminate control practices.

Figure 1
Graphic representation of ecological niches occupied by man and wolves, indicating possible management scenarios (drawing by Andrew Raszewski)

Figure 1



The relationships among man, wolves, and prey are the factors that have to be considered in a management strategy. Both man and wolves are predators and share a common ecological niche. Hence the pragmatic management solution is to arrange for the two species of "predators" to co-exist. This is the essence of wildlife management and conservation policy today, difficult though it is to put into practice.

At the same time, despite a rising tide of anti-hunting sentiments, the number of hunters increased. Frontier areas were being opened, leisure time was increasing, and access to modern technology, such as rifles and mechanized all-terrain vehicles, placed renewed pressures on ungulate populations. For these reasons, and possibly in combination with a variety of others (notably severe winters), ungulate populations have declined in many parts of North America, for example, caribou in the Arctic, deer in eastern Canada and northeastern US, and moose in parts of Alaska and Canada. The available ungulate prey base, therefore, has been subjected to ever-increasing losses. Hunters in some instances have blamed wolves for the declines; environmentalists blame hunters; biologists state that it is often a combination of both. The issue is clouded by value judgements coming from every quarter. Such debates place a responsibility on the scientific community to generate information that can be used for the management of both wolves and ungulates.

Figure 1 illustrates the various possibilities for different management options. These range from unmanipulated predator–prey systems through one that is man-dominated to one that may be the pragmatic management solution that permits man, wolf, and prey to co-exist. This is the essence of wildlife management and conservation strategy today, difficult though it sometimes is to put into practice.

Research on wolves in North America began with naturalistic studies by Murie at Mount McKinley National Park, Alaska, in the early 1940s. Studies continued into the 1950s and 1960s. Within the last decade, man's ability to study predator–prey systems has been greatly enhanced through the use of radio-telemetry. Biologists have become more aware of some of the details and quantitative aspects of predator–prey interactions (see Keith, this publication). We now know, for example, that predation by wolves, particularly in single prey systems, can be an important limiting factor. The long-term implications of naturally occurring predator–prey oscillations and of interactions with habitat are less clearly understood and only time and research will give us answers to some of those questions.

Science is self-correcting. In some cases current findings partially vindicate those who had all along blamed the wolf for ungulate declines. However, to cry "wolf" simplifies a complex issue, as does the echo that now cries "hunter". Long-term studies such as those being carried out in Riding Mountain National Park (Manitoba), or Isle Royale (Michigan) and in Minnesota caution us not to jump to conclusions and it appears that the socio-political issues become more complex as biological information expands.

In recent years emphasis has increasingly been placed on developing conservation strategies. The International Union for the Conservation of Nature and Natural Resources (IUCN) has developed a World Conservation Strategy. In Canada, national and provincial conservation strategies are in various stages of completion. A logical first step in dealing with the future conservation and management of the wolf is to delineate its current distribution. Therefore this meeting of wolf specialists at the symposium in Edmonton was timely.

The purpose of the meeting was to document the status of wolves in Canada, and to discuss some of the problems related to their conservation. The Canadian population runs as a continuum with wolves in Alaska and to a lesser extent with adjacent areas in Montana and Minnesota. The report that resulted from the symposium was designed to be of use for the layman (be he a naturalist, hunter, or farmer) and for the scientist, who is always attempting to extend the frontiers of knowledge. Scientists have a responsibility to communicate findings to their peers and to the public. This publication is designed to do both. The layman will find the papers on status of the species, the management programs relating to interpretation in parks, and wolf–livestock interactions of more immediate interest. Technical papers on genetics, population dynamics, taxonomy, and behaviour probably appeal to a more restricted readership. Several papers have elements of interest to both readerships. For example, the layman may find the section on human-caused population changes of considerable interest but may have little concern for the taxonomy of subspecies. The emphasis in status reports was placed on distribution maps, historical records of abundance, and the identification of specific problem areas, such as zones of wolf–livestock interactions. These reports will serve as benchmarks against which changes in the distribution of the species can be evaluated in the future. A survey of the taxonomic status of wolves provided an interesting background for the regional reports. The remaining papers deal with a variety of topics; however, several themes relating to wolf management, conservation, and basic biology predominate — three papers deal with wolf–livestock problems, two with wolf–ungulate interactions, and one with wolf–wilderness relationships as perceived by park visitors. The paper on differentiation of wolf and dog tracks is a worthwhile contribution to a problem that becomes important where wolves appear at the fringes of their current ranges. Two papers from Alaska deal with wolf-harvesting methods on the Kenai peninsula and with the socio-political aspects of wolf management.

Because of the complexity of the problem and the lack of empirical evidence, the first paper on genetics turned out to be a controversial one when subjected to peer group review. Nonetheless, with the author's permission, the paper is retained; it stimulated a lively debate and prompted the inclusion of an alternative view (see Shields, this publication). The paper on social influences on reproduction in wolves touches on a subject that will be important in the management of the predator.

Probably more is known about the biology of wolves than of any other North American large carnivore. However, we are still at a very preliminary stage in being able to apply our knowledge to the effective management of the species in a way that will ensure its survival, yet deal with the practical problems related to conflicts with man's consumptive interests.

The symposium was promoted by IUCN/Species Survival Commission. I extend my appreciation to L.D. Mech (Chairman of the SSC Wolf Group) for his co-operation. The workshop was financially supported by a private donor and by the Canadian Wolf Defenders. Various agencies (see colophon page) contributed towards the production costs of this Report. Logistical and administrative services were channelled through the Boreal Institute, University of Alberta, and I thank R. Jamieson, Director, and A. Moore, Administrative Assistant, for their support. H. Cleator, D. Meleshko, and M. Ramsay, three zoology students from the University of Alberta, are thanked for taping the proceedings and assisting in numerous ways. I thank J. Gunson, N. Novakowski, and P. Paquet for their helpful advice. My sincere gratitude is extended to E. Telfer, whose support and encouragement made it all possible. All papers were reviewed by two or more referees and their valuable contributions are gratefully acknowledged. The Scientific and Technical Editing Section of the Canadian Wildlife Service (particularly P. Loshak) handled final editing and production. I wish to acknowledge the assistance of the staff of Parks Canada, both for their efforts to promote wolf research in Canada and for providing me with time and encouragement to undertake the organization of this symposium.

Status

Photo: Scot Stewart

A perspective on the taxonomy of wolves in North America

Ronald M. Nowak

1. Abstract

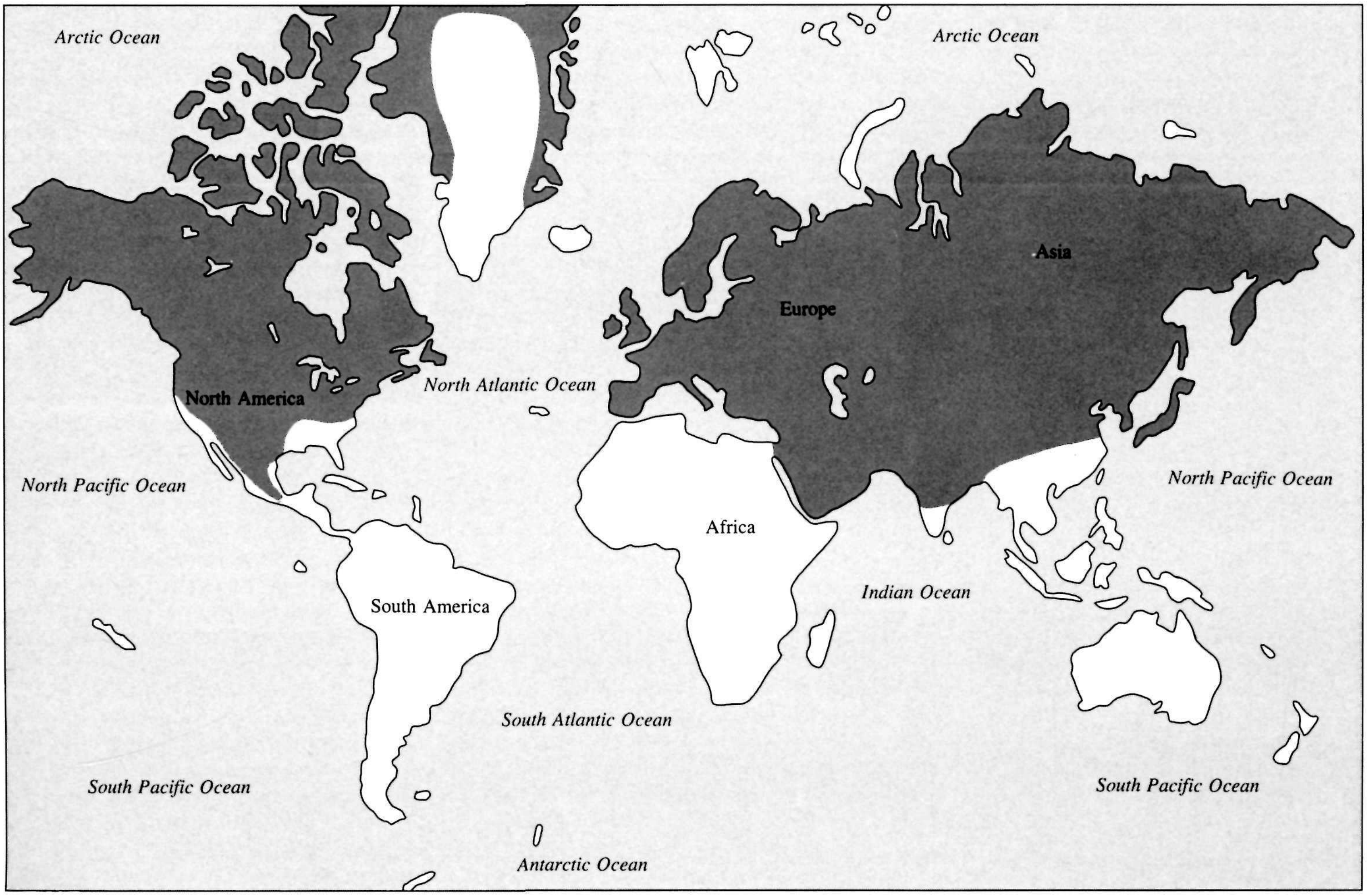
The grey wolf is among the most variable and widely distributed of mammals. In North America 24 subspecies are currently recognized, though recent studies imply this number should be reduced. A bivariate analysis of 363 skulls, representing 19 subspecies, supports earlier suggestions that affinity occurs mainly in an east–west direction, and that there is a pronounced character change in the area of the border between Canada and the conterminous United States. It is hypothesized that a wolf population, isolated in Alaska by late Pleistocene glaciation, spread eastward following withdrawal of the ice sheet, and gave rise to most of the present subspecies of Alaska and western Canada. Another Pleistocene group, found to the south of the ice, would have developed into the subspecies of most of the conterminous US and the upper Great Lakes region. The wolf was evidently exterminated in the northwestern conterminous US by the 1940s. Specimens subsequently collected in that region resemble the wolves now found in Alaska and western Canada.

2. Introduction

The grey wolf (*Canis lupus*) has the greatest natural range (Fig. 1) of any living mammal other than *Homo sapiens*. Except for man, the only mammalian species that has ever had a more extensive natural range is the lion (*Panthera leo*). In the late Pleistocene and early

Figure 1
Original worldwide distribution of wolves (shaded area)

Figure 1



Recent epochs the lion, also a large, highly adaptable, group-living carnivore, occupied much the same regions as the wolf does now, plus Africa and northern South America (Hemmer 1974).

The grey wolf is an unusually variable species, both geographically and individually. This characteristic has been passed on to, and intensified in, the domestic dog, which was apparently derived from one of the small south Eurasian subspecies of *C. lupus*. The presence of relatively small forms of wolves all along the southern periphery of the wolf's range has provided the most consistent difficulties with the systematics of the group. In North America these small forms include the Mexican wolf (*C. lupus baileyi*), the "Algonquin type" of *C. lupus lycaon* described by Kolenosky and Standfield (1975); and the red wolf (*C. rufus*) of the southeast. This last animal is the only living wolf that most authorities consider to be a species distinct from *C. lupus* (Nowak 1979).

In the Old World the small extinct Japanese wolf, *C. hodophilax*, is also sometimes called a separate species (Imaizumi 1970*a*, *b*), and a very small extinct subspecies of southern Spain (*C. lupus deitanus*) may actually have been a kind of jackal (Pocock 1935). Even disregarding these two forms, however, the variability of *C. lupus* seems to be more pronounced in Eurasia than in North America. Figure 2 shows how measurements of zygomatic width of skull vary between Russian wolves (Novikov 1962) and the subspecies *C. lupus arabs* of the Arabian Peninsula (Harrison 1968). Figure 2 also shows measurements for a large, a medium-sized, and the smallest North American subspecies of *C. lupus* (Nowak 1973). Considerably less variation is evident in the North American specimens. When, however, the same measurements of the red wolf and coyote (*Canis latrans*) are compared, the full character gradient in North America is seen to be approximately equal to that in the Old World. Perhaps if the coyote and red wolf were not present, some of our grey wolves would be as small as those in parts of Eurasia.

3. Subspeciation in the grey wolf

The main concern of this paper is the intraspecific relationships of the North American grey wolf. The 24 subspecies now recognized on the continent (Fig. 3) are based largely on the work of Goldman (1944). However, he did not employ statistical analysis or any modern taxonomic methods. He had relatively few specimens from some regions, especially Canada, and much larger collections have since become available (the most important ones being those of the University of Alaska, the University of British Columbia, the Ontario Ministry of Natural Resources, the National Museums of Canada, and the Provincial Museums of both British Columbia and Alberta).

A number of challenges to Goldman's scheme have been made in the last three decades. For example, recent studies by Michael Bogan (pers. comm.) and others at the US National Museum of Natural History suggest that the subspecies *monstrabilis* and *mogollonensis* are not separate from *baileyi*. Rausch (1953) thought that the Alaskan subspecies *tundrarum* and *pambasileus* could not be distinguished from each other by the criteria given by Goldman. Rausch also questioned the validity of *alces* of the Alaskan Kenai Peninsula, of which Goldman had only five specimens. The status of *alces* is complicated by the likelihood that the original Kenai population became extinct just after the turn of the century, and that wolves later moved back into the area from the range of another subspecies. We find this same kind of problem reappearing in other areas of systematic investigation.

Kelsall (1968) suggested that subspecific boundaries in north-central Canada [later portrayed by Hall (1981)] are meaningless. He noted that the wolves from the areas designated for *mackenzii* and *hudsonicus* annually invade the areas normally inhabited by *occidentalis* and

Figure 2

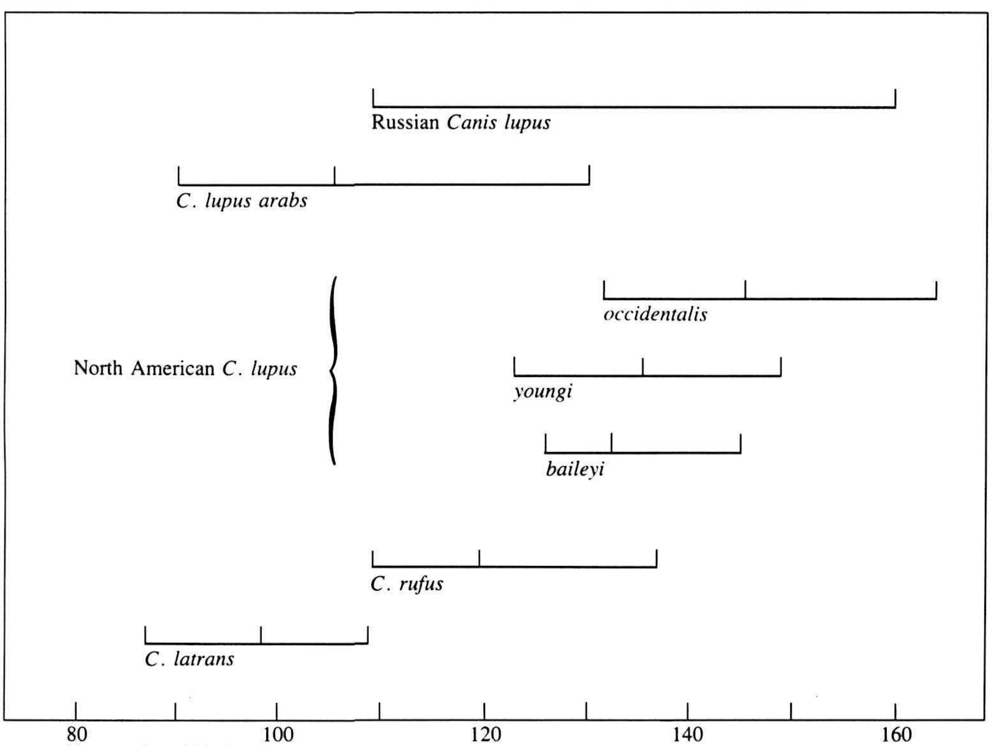


Figure 2
Zygomatic widths of skulls of wolves and coyotes. Horizontal lines show range; vertical lines within ranges show means

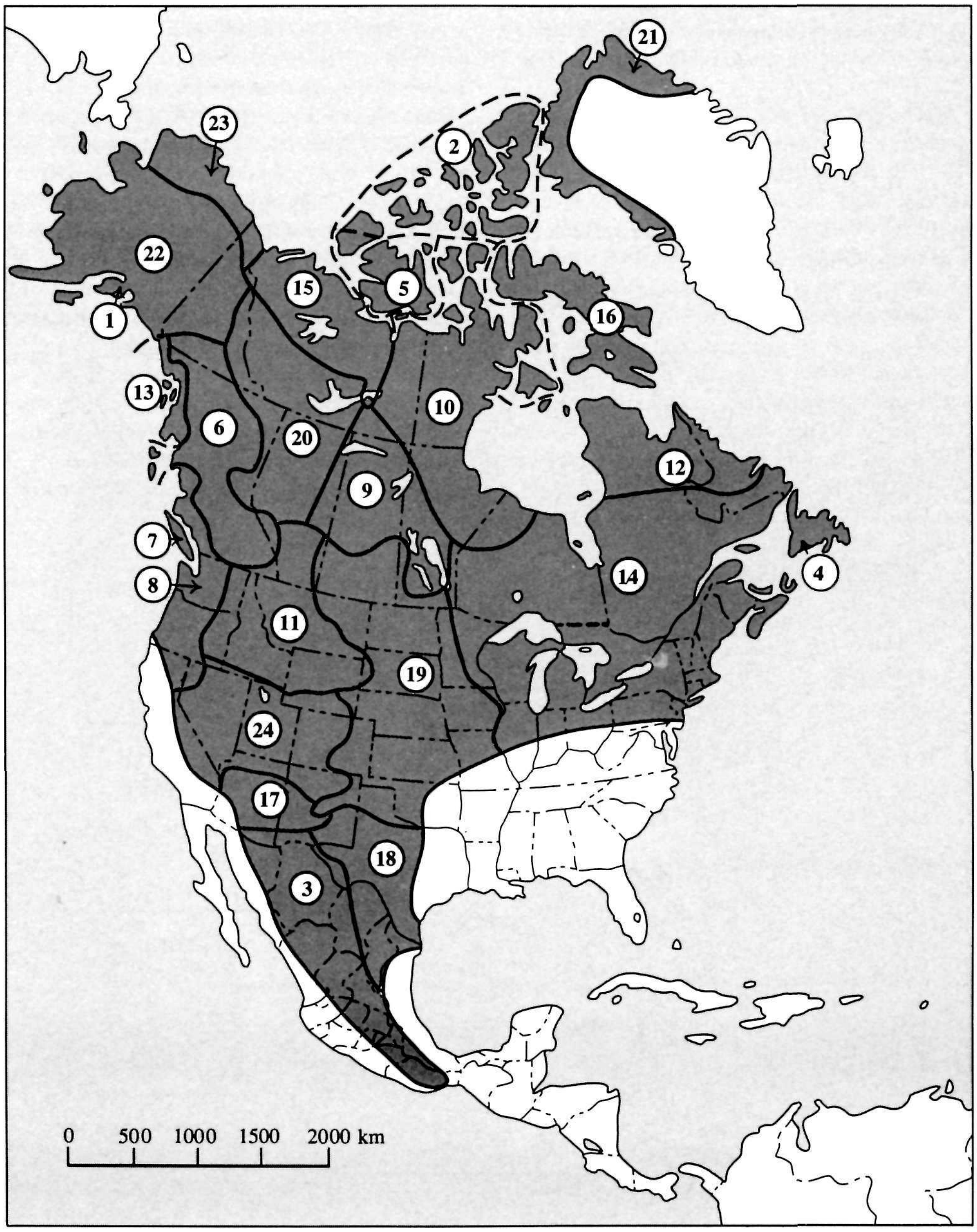
Figure 3
Distribution of currently recognized subspecies of *Canis lupus* in North America. Current range is considerably reduced from the historical range shown in Figure 8

griseoalbus, following caribou (*Rangifer tarandus*) herds for hundreds of miles. Banfield (1974) stated that the number of subspecies in Canada might be "drastically reduced in future studies". Jolicoeur (1959) did a multivariate analysis of nearly 500 wolf skulls from western Canada and Alaska, and concluded "The overall pattern of variation between the populations sampled is more suggestive of an incompletely panmictic continuum than of distinct subspecific units". Although he postponed taxonomic conclusions pending the availability of more material, he thought that far too many subspecific names were in use. He found only one population, that of *crassodon* on Vancouver Island, to be sharply different from its immediate neighbours. Interestingly, however, more recent studies have suggested that the differences between *crassodon* and mainland populations are too minute to justify subspecific distinction (letter from Mark Angelo, British Columbia Institute of Technology, to L. David Mech, US Fish and Wildlife Service, 13 January 1977). Vancouver Island is another place where wolves apparently became very rare early in the 20th century and then moved back from other areas.

Although most recent work has indicated that the number of subspecies should be reduced, at least one study has hinted at the possible need for a new line. Kolenosky and Standfield (1975) distinguished between a northern "Boreal type" and a southern "Algonquin type" within the currently recognized subspecies *lycaon*. They reported that "the ranges of the two types overlap throughout a broad band across east-central Ontario, but there is no conclusive evidence of their interbreeding" (the approximate ranges of the two are divided by the dashed line in Fig. 3). These authors found significant morphological differences between the two, the Boreal type being larger and more massive; 75% of the specimens of the Boreal type could be completely separated from the Algonquin type.

The implications of Kolenosky and Standfield's work could be substantial. Although my own studies (Nowak 1979) indicated much overlap between the various populations of *lycaon*, my sample was small and my approach was quite different from theirs.

Figure 3



1 *Canis lupus alces*	**7** *C.l. crassodon*	**13** *C.l. ligoni*	**19** *C.l. nubilus*
2 *C.l. arctos*	**8** *C.l. fuscus*	**14** *C.l. lycaon*	**20** *C.l. occidentalis*
3 *C.l. baileyi*	**9** *C.l. griseoalbus*	**15** *C.l. mackenzii*	**21** *C.l. orion*
4 *C.l. beothucus*	**10** *C.l. hudsonicus*	**16** *C.l. manningi*	**22** *C.l. pambasileus*
5 *C.l. bernardi*	**11** *C.l. irremotus*	**17** *C.l. mogollonensis*	**23** *C.l. tundrarum*
6 *C.l. columbianus*	**12** *C.l. labradorius*	**18** *C.l. monstrabilis*	**24** *C.l. youngi*

Source: adapted from Hall 1981.

Figure 4
Multivariate stepwise discriminant analysis comparing skulls of the species *Canis rufus* (R) and certain subspecies of *C. lupus* (other letters). Only males are shown, and only marginal positions of each group are plotted (for explanation of procedure, see Nowak 1979)

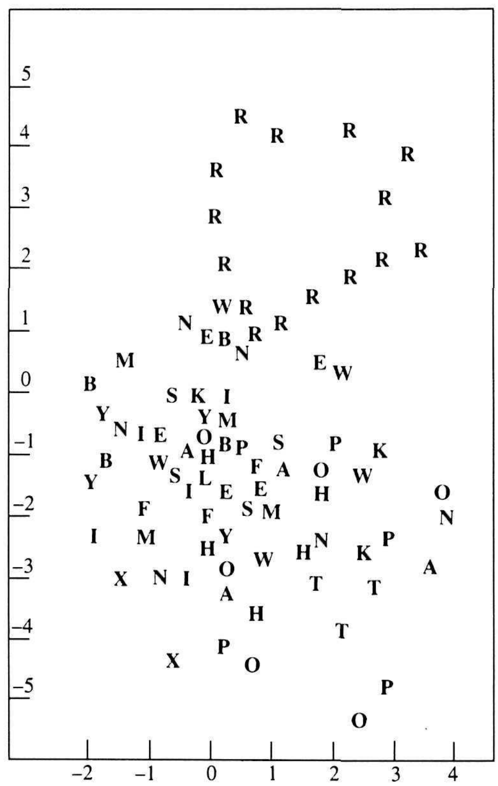
Their statement regarding the wide separation and even lack of interbreeding between their two types of *lycaon* raises the possibility of an affinity between the small Algonquin type and its southern neighbour, the red wolf.

The above discussion shows the considerable disagreement and confusion that still exist in wolf taxonomy. I think part of the difficulty is that the term "subspecies", particularly as applied to *C. lupus*, is often misunderstood. Some consider that to be called a subspecies a wolf population must be fairly distinct in size, proportion, or colour pattern. I am often asked to identify a subspecies based on a single specimen, sometimes consisting only of a skin, a live animal, a bone fragment, or even a photograph. Such identification is hardly ever possible, because subspecific names usually represent only averages or trends that supposedly occur in a geographic area. There is usually considerable overlap between the characteristics of neighbouring subspecies, and some specimens found well within the range of one named group may be practically identical to some specimens from the ranges of other named groups.

It has been said that species are created by God, but that other taxonomic categories, including subspecies, are devised in the human mind. Designation of subspecies may depend on the views of the taxonomist concerned, the time that can be devoted to a project, the quantity and geographic extent of available specimens, and the study methods employed. Two workers may arrive at two quite different arrangements of subspecies. Some taxonomists apply subspecific names whenever they think average differences become sufficiently pronounced, even along a gradual cline. Others think that subspecies should be designated only if a sharp shift in characters occurs across a relatively narrow geographic zone. Still others do not like to use subspecific designations at all, and prefer to express variation within a species in some other manner.

In my own opinion, after having measured thousands of wolf skulls taken throughout North America, Goldman did a remarkably good job with the material available to him. If I were to repeat his work, however, I would probably accept what most recent authorities

Figure 4



Source: Nowak 1973

suggest, and draw fewer subspecific lines, if any. I have never thoroughly examined the intraspecific relationships of the grey wolf. Figure 4 is based on a multivariate stepwise discriminant analysis of 15 cranial measurements. The red wolf and 15 subspecies of *C. lupus* are compared. Only the positions of the specimens of *C. rufus* (marked as R) stand out from the others. There is extensive overlap among the subspecies of *C. lupus*, providing little basis for simplified groupings.

4. Reassessment of affinities

How can this be sorted out and an effort made to bring the taxonomy of the grey wolf up to date? A good place to start might be with the study by Skeel and Carbyn (1977) of systematic relationships of wolves in four national parks of Canada. Figure 5 is taken from their paper, and shows the location of specimens used in a multivariate analysis of 15 cranial measurements. Briefly summarized, the analysis indicated affinity in east–west directions: the subspecies *irremotus* (I), *nubilus* (N), and *lycaon* (L) appeared closely related and to have little affinity with the three samples taken from just to the north (J, P, R), within the range of the subspecies *occidentalis* and *griseoalbus*. The three samples also showed close affinity to one another. The two samples from farther north (W, H) were also more similar to each other than to the other subspecies.

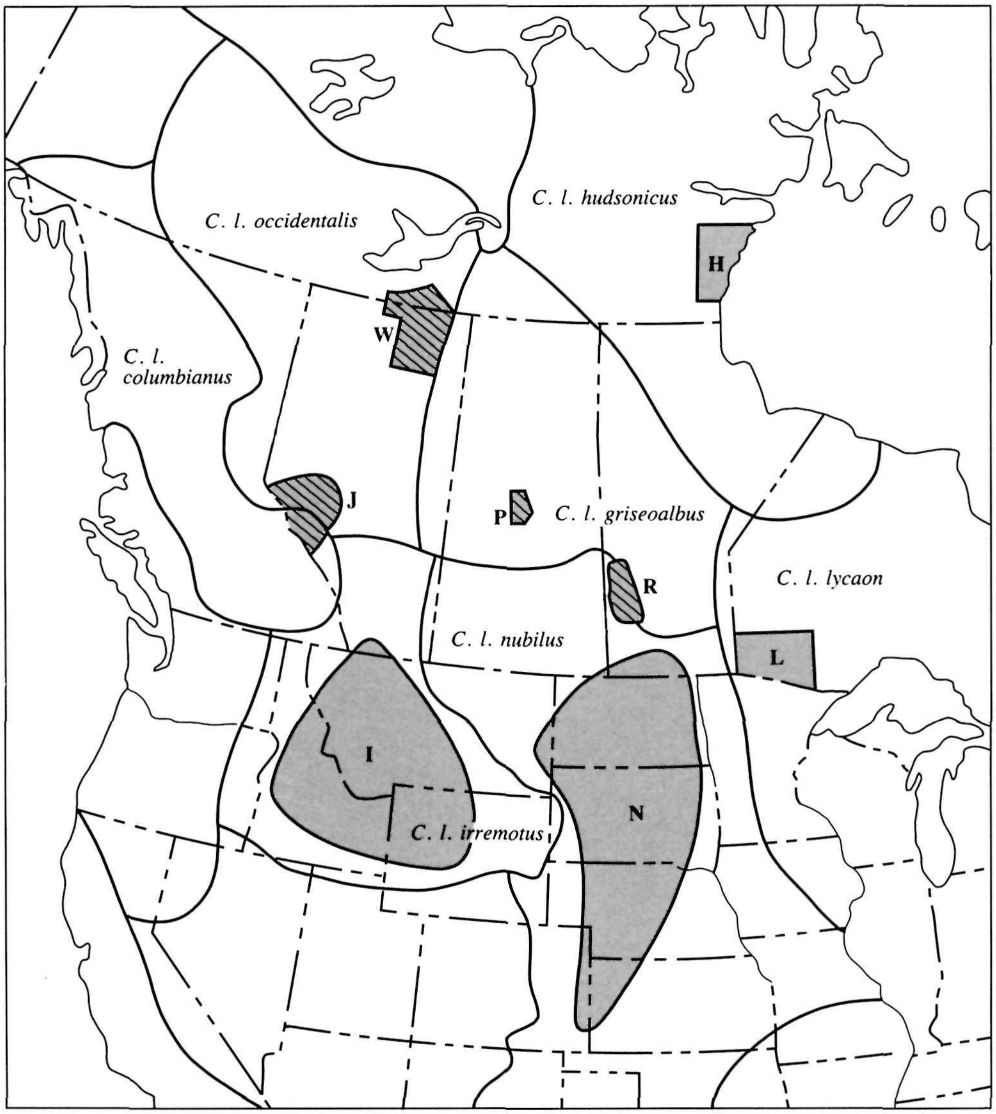
Skeel and Carbyn's study suggests to me that there may be a fairly sharp shift in characters of *C. lupus* in a zone that covers much of the US–Canada border area and then swings northward in western Ontario. Perhaps it is here that some future worker will draw a line dividing one subspecies covering a large part of Canada from another occupying much of the conterminous US, as well as the western Great Lakes region of Canada. That there might be some affinity between the wolves of the Great Plains and those of the western Great Lakes region was suggested earlier by Mech and Frenzel (1971).

I have long wondered about the possibility of some kind of distinction along the lines suggested above. I have only had opportunity, however, to prepare a cursory bivariate analysis. The two measurements used were greatest length of skull and length of P4. Only males were measured, representing 19 subspecies (the name and sample size of each are given in the legend of Figure 6). It is important to note that the sample of *lycaon* is entirely from the region of Ontario within the range of the Boreal type discussed by Kolenosky and Standfield (1975) and from nearby parts of Minnesota and the upper peninsula of Michigan. Figure 6 shows only the mean positions of each subspecies; this approach is inadequate, but is intended only to suggest a possible arrangement for future investigation. The analysis does produce a picture that corresponds with the impression I have received over the years from the examination of numerous wolf skulls.

Figure 5
Range distribution of specimens obtained in a study on wolf taxonomy in Canadian national parks

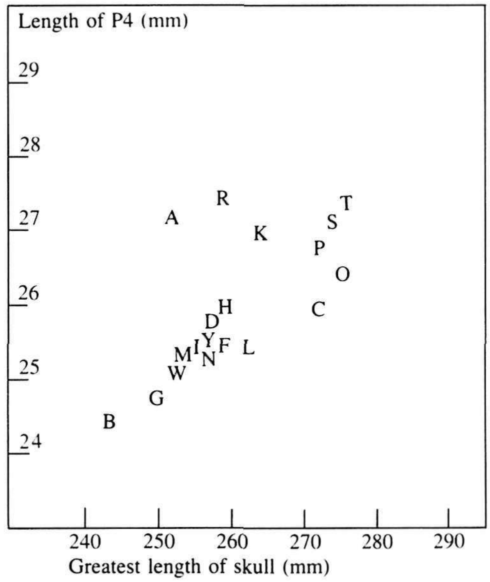
Figure 6
Bivariate analysis of measurements of the skulls of males of 19 subspecies of *Canis lupus*, showing relationship of skull length to P4

Figure 5



P Prince Albert National Park
R Riding Mountain National Park and vicinity
J Jasper National Park – Edson area
W Wood Buffalo National Park
N *Canis lupus nubilus*
I *C. l. irremotus*
L *C. l. lycaon*
H *C. l. hudsonicus*

Figure 6



A *Canis lupus arctos* (N = 14)
B *C. l. baileyi* (N = 19)
C *C. l. columbianus* (N = 10)
D *C. l. crassodon* (N = 8)
F *C. l. fuscus* (N = 10)
G *C. l. mogollonensis* (N = 18)
H *C. l. hudsonicus* (N = 11)
I *C. l. irremotus* (N = 15)
K *C. l. mackenzii* (N = 5)
L *C. l. ligoni* (N = 26)
M *C. l. monstrabilis* (N = 10)
N *C. l. nubilus* (N = 24)
O *C. l. occidentalis* (N = 37)
P *C. l. pambasileus* (N = 20)
R *C. l. bernardi* (N = 6)
S *C. l. griseoalbus* (N = 8)
T *C. l. tundrarum* (N = 14)
W Western *C. l. lycaon* (N = 84)
Y *C. l. youngi* (N = 24)

Source: reprinted with permission from Can. J. Zool, Vol. 55, p. 740

Canis lupus columbianus, one of the larger subspecies of wolves, photographed in Jasper National Park (photo: H. Fuhrer)

Figure 6 shows a general cline in size from the small southern subspecies *baileyi* to the large subspecies of Alaska and northwestern Canada. There have been suggestions that the differences between these populations of grey wolves merely reflect the size of the predominant prey species. Undoubtedly this is a factor, but the largest prey of all, the bison (*Bison bison*), was a major food item of the subspecies *nubilus*, which was not an especially large wolf. Also, wolves that feed extensively on deer (*Odocoileus* spp.) may be either fairly large, like *ligoni* of southeastern Alaska, or small, like the Algonquin type of *lycaon*. Wolves that prey on moose (*Alces alces*) may be either large, like *pambasileus*, or medium-sized, like those on Isle Royale (some specimens of which are in my sample of western *lycaon*).

In Figure 6, the means of the subspecies that occupy most of Alaska and inland western Canada (*tundrarum*, *pambasileus*, *occidentalis*, *columbianus*, and *griseoalbus*) fall relatively close together. Another cluster is formed by the means of the subspecies that occur in the mountains and plains of the western US (*irremotus*, *youngi*, *nubilus*, and *monstrabilis*), in the Great Lakes region (western *lycaon*), and along the Pacific coast of the US and southwestern Canada (*fuscus* and *crassodon*). The subspecies of the southeastern panhandle of Alaska (*ligoni*) is not far removed from this cluster. The small southern subspecies (*baileyi*) stands somewhat apart from the other wolves of the western US. *C. hudsonicus* of north-central Canada is, on this graph, closer to most US wolves than to its neighbours in Canada, but this position may reflect my small sample size and failure to consider more characters.

The subspecies *mackenzii* of the Arctic coast of Canada seems intermediate to the large mainland subspecies and the wolves of the High Arctic islands. The latter (*arctos* and *bernardi*) fall outside the main character gradient shown on the graph. This position reflects the relatively short skulls and large teeth of the animals. Jolicoeur (1959, 1975) suggested that this condition might be caused partly by environmental factors; the long, hard winter could prevent the skull from reaching full growth potential. He did, however, think that evolutionary factors were also involved. The skulls of some of these Arctic wolves resemble those of certain late Pleistocene *C. lupus* from the Rancho La Brea Tar Pits of California (Nowak 1979). In both cases there is a tendency for the skull to be very broad and the teeth to be large relative to total length of skull. Perhaps there was once a continuous population of such wolves that was driven by Pleistocene glaciation both southward as far as California, where it eventually disappeared, and northeastward into the Pearyland Refugium of northern Greenland.

The movements of the late Pleistocene ice sheets may have much to do with current wolf systematics. Figure 7*a* shows the maximum extent of glaciation, with hypothetical survival of wolf populations in the ice-free areas of the central US, northern Greenland, and Alaska (then connected to Siberia). Withdrawal of the glaciers at the end of the Pleistocene may have led to a spread of the Greenland population across much of the Arctic, of the Alaska–Siberia population into western and central Canada, and of the central US population into the mountains and plains of the West and the western Great Lakes region. Another wolf population may have been isolated to the southeast — both by glaciers and the presence of the red wolf to the south. This population would have moved into the eastern Great Lakes region following withdrawal of the ice, and eventually might have moved farther when white-tailed deer (*Odocoileus virginianus*) extended their range northward in the late 19th century (Kolenosky and Standfield 1975). Meanwhile, the subspecies *baileyi* may have been isolated to some extent by desert barriers in the southwest. There is no question that very small grey wolves existed in Mexico during the Pleistocene. The smallest North American skull of *C. lupus* that I have seen was collected from the San Josecito Cave deposits in central Nuevo Leon (Nowak 1979). The same site contained remains of dire wolves (*C. dirus*), coyotes, and an undescribed species of *Cuon*, the genus of dholes or hunting dogs, now confined to Asia.

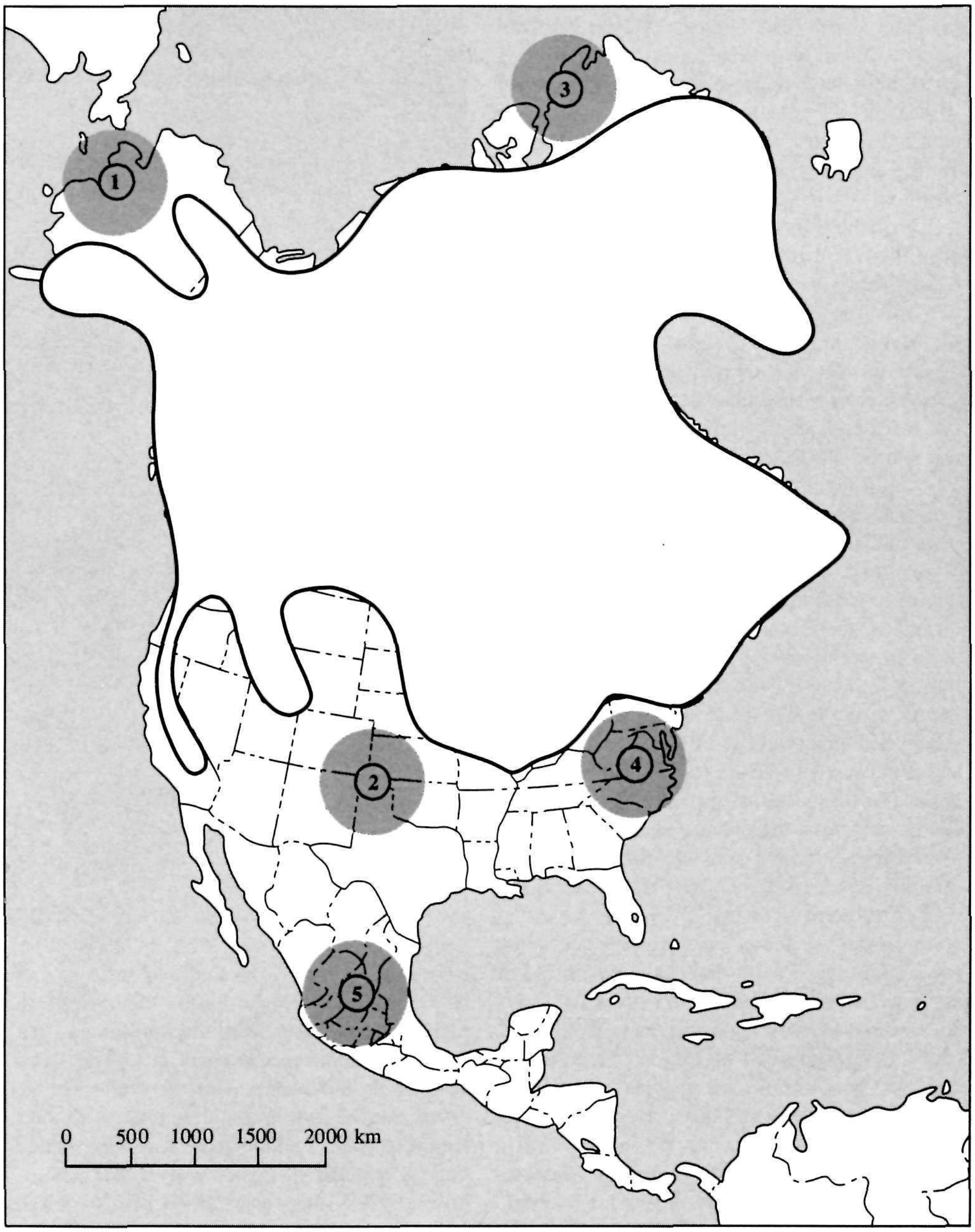
Based on these geological speculations, and my cursory examination of wolf specimens, one possible systematic arrangement of North American *C. lupus* would be as shown in Figure 7*b*. There is a main northern group, consisting of related wolves that were all derived from the stock isolated to the northwest of the glaciation, a main southern group representing the wolves that were isolated to the south, an Arctic group descended from the wolves of the Pearyland Refugium, the eastern or Algonquin type of *lycaon*, and the small *baileyi* of the southwest. Inclusion of the northeastern Canadian subspecies (*manningi*, *labradorius*, and *beothucus*) in my main northern group is purely arbitrary, as very few specimens were available to me; possibly these populations (and even *hudsonicus*, just to the west) have more affinity to my main southern group. Otherwise, the lines shown on the map correspond to zones where character shifts seem evident. I cannot now say if the 24 currently recognized North American subspecies should be reduced to 5 that fit the groupings shown, and certainly many problems and questions remain. Nonetheless, Figure 7*b* presents a hypothetical framework that some future investigator could use in attempting a systematic revision of *C. lupus*.

5. Human-caused systematic changes

One problem that any future taxonomist will have is that few new wolf specimens will be forthcoming from many areas. Nearly half of the currently recognized subspecies may already

Figure 7*a*
Maximum extent of Pleistocene glaciation in North America. Shaded areas show hypothetical areas of survival of wolf populations

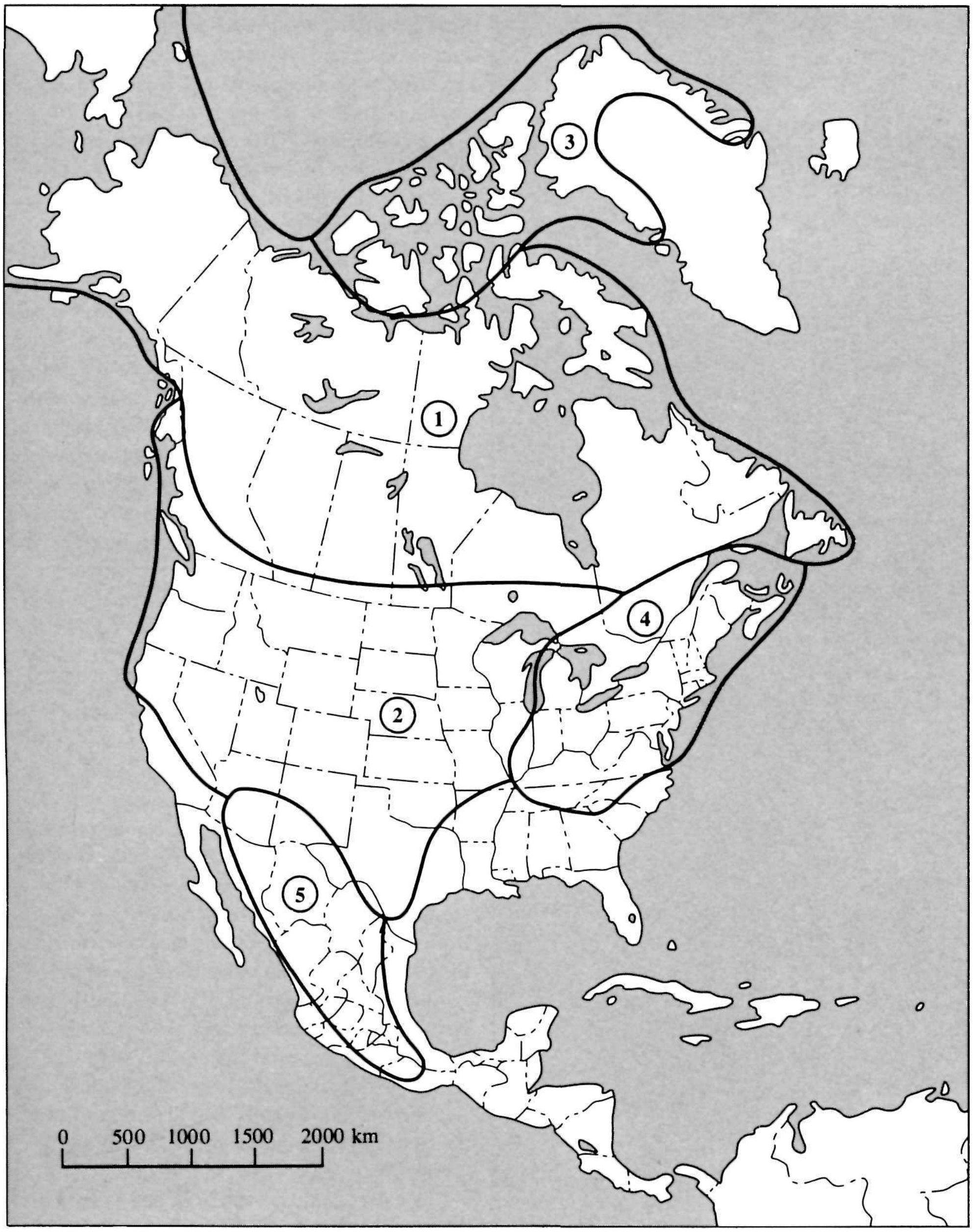
Figure 7*a*



1 Northern group
2 Southern group
3 *Canis lupis arctos*
4 Eastern *C. l. lycaon*
5 *C. l. baileyi*

Figure 7*b*
Hypothetical distribution of wolves following withdrawal of Pleistocene glaciation

Figure 7*b*



1 Northern group
2 Southern group
3 *Canis lupis arctos*
4 Eastern *C. l. lycaon*
5 *C. l. baileyi*

be extinct. Some of the designated ranges of these subspecies have been invaded by wolves from the ranges of other subspecies. Even on the Arctic islands wolves have declined; both the subspecies *orion* of Greenland and *bernardi* of Banks and Victoria islands may have been eliminated and their ranges partly occupied by the subspecies *arctos* (Nowak, R.M., The gray wolf in North America, unpubl. rep. to New York Zool. Soc. and US Bur. Sport Fish. Wildl. 1974).

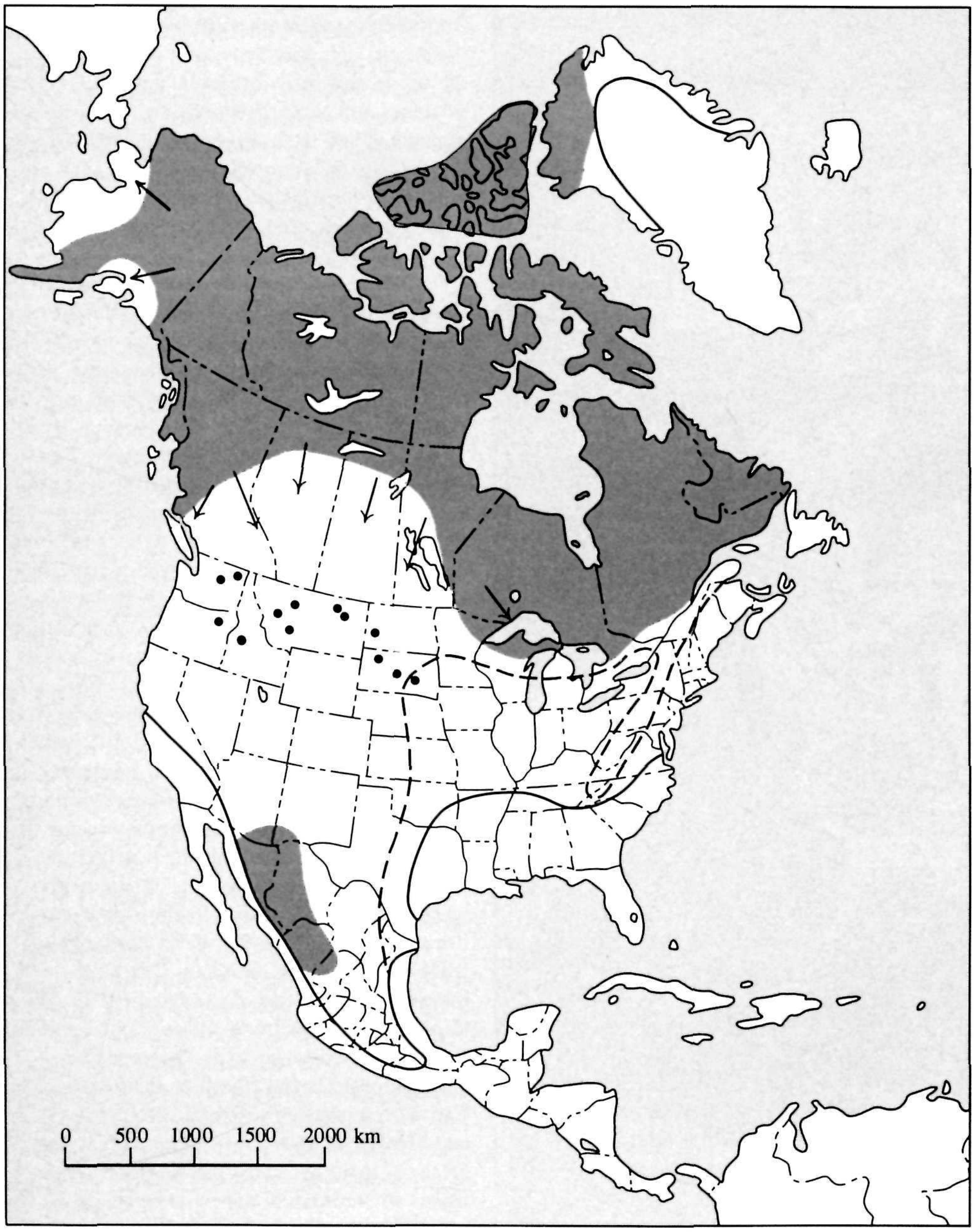
Figure 8 shows the general course of the decline of the grey wolf in North America (Young 1944, Nowak 1975). By about 1900 the species had disappeared from the eastern half of the US, except for parts of the Appalachian chain and the upper Great Lakes region. By 1930, after the West filled with livestock and after massive government, corporate, and private control efforts, there was reason to think that the grey wolf was nearing extinction. It had disappeared from nearly the entire western half of the US and much of southwestern Canada. Even in the heart of its remaining range, serious declines were reported in its main prey species, the caribou.

Then, from the 1930s to the early 1950s, there was a dramatic reversal. Several causes have been suggested — a drop in fur values resulting from the Great Depression, distraction of people and governments because of World War II, and better game management resulting in more prey species. Whatever the reason, it was one of the most remarkable wildlife comebacks in history. In a sweeping arc from Alaska, where they moved on to the ranges of the introduced reindeer herds, to the Great Lakes, where they crossed the ice to Isle Royale, the wolves spread. The greatest increases appear to have been in southwestern Canada, especially in Alberta, Saskatchewan, and Manitoba, where the wolf reclaimed vast areas of its former range and was seen again in places where it could not be remembered by local people.

Human reaction was swift and hard-hitting. Large scale control programs were instituted in both Alaska and Canada, and the advance of the wolf was stopped. However, since that period the distribution of the grey

Figure 8
Declining distribution of wolves and limits of their range

Figure 8



——— Original range of *Canis lupus*
– – – – Range in 1900
▓ Range in 1930

Dots indicate localities at which specimens of *Canis lupus*, examined by the author, were collected between 1941 and 1978 in the northwestern conterminous US. Arrows show modern range extensions.

wolf has remained relatively stable, and the 300-year pattern of steady decline appears to have been broken. It must be added, though, that losses of certain resident populations have occurred since then, most notably on several Arctic islands, in the upper peninsula of Michigan and northern Wisconsin, in the Cascade Mountains of Oregon, and in the US–Mexican border region. The Mexican wolf has continued to decline and currently only a few dozen individuals of this subspecies may remain.

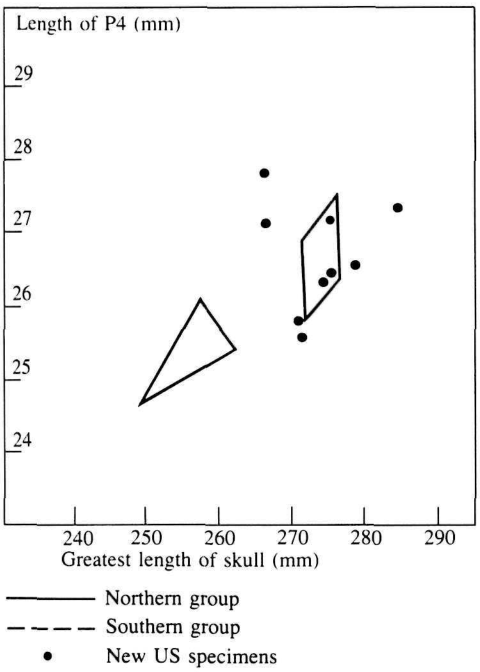
During and after the increase of wolves in western Canada, individuals and small groups were again reported in the northwestern US. It is now evident that some wolves are regularly present in this region, especially western Montana (Ream 1980, Annu. Rep., Wolf ecology, Univ. of Montana). There has long been a question as to whether these animals represent survival of the populations that originally inhabited US territory or are invaders from Canada.

I suggested above that perhaps the wolves of much of the continent could be divided, roughly at the US–Canadian border, into main northern and southern groups, the northern animals averaging a considerably larger size. Figure 9 represents a bivariate analysis of greatest length of skull to P4 length of males and shows the boundaries of the mean positions of northern subspecies (*tundrarum*, *griseoalbus*, *pambasileus*, *occidentalis*, and *columbianus*) and southern subspecies (*ligoni*, *crassodon*, *fuscus*, *youngi*, *irremotus*, *nubilus*, *monstrabilis*, *mogollonensis*, and western *lycaon*), as taken from Figure 6. In Figure 9 I have drawn only the boundaries of the mean positions of the northern and southern groups. The individual positions of nine undamaged skulls of full-grown males, taken in the northwestern conterminous US since 1941, are also plotted. The positions of these skulls all fall within or near the boundaries of the means of the northern group.

As my study was brief and based on so few characters, no definitive statements can be made about the origin of wolves now occurring in the western US. This problem and the subject of over-all intraspecific relationships of the grey wolf remain areas where further research is needed.

Figure 9
Bivariate analysis of measurements of the skulls of male wolves

Figure 9



The solid line encloses the mean positions of the subspecies indicated by the symbols T, S, P, O, and C in Figure 6. The dashed line encloses the mean positions of the subspecies indicated by the symbols G, W, M, I, N, Y, D, F, and L in Figure 6. Dots indicate positions of nine male specimens collected in the northwestern conterminous US between 1941 and 1978.

Status and management of wolves in British Columbia

Frank S. Tompa

1. Abstract

The history of wolf management in BC is described. Indiscriminate wolf control during the first half of the century caused near extinction of the species on Vancouver Island, and a substantial decline in mainland populations. Wolves have recovered throughout the Province since protective regulations were introduced during the 1960s. The wolf now has big game and fur-bearer status and is completely protected in all National and some Provincial Parks. Control is directed only at wolves that attack livestock or threaten human safety. Out of an estimated provincial population of 6300, 200–450 are harvested annually by trapping and hunting, and 50–200 by control.

2. History

Historic records of the wolf (*Canis lupus*) from British Columbia are scarce. Abundant wolf and declining deer (*Odocoileus hemionus columbianus*) populations were reported in the early 1900s from Vancouver Island (Provincial Game Warden reports 1905–28). Wolves did not have game status and were increasingly persecuted through bounty hunting, and in later years through poisoning. Subsequently the reports refer to declining wolf populations and by the 1920s the species had become scarce on the island.

The Game Warden's reports do not provide reliable numerical information on mainland wolf populations. Although wolves were present throughout the Province, with the exception of the southernmost areas, they were apparently nowhere abundant before the turn of the century. However, the annual Game Warden reports and the Provincial Game Commission reports (1929–55) refer to increasing wolf populations in the northern regions and the central interior from the early 1920s until the late 1940s. It is assumed that the reported increase was real and followed a gradual spread of moose (*Alces alces*) throughout the Province (Preliminary Moose Management Plan 1979, Min. of Environ., BC).

The increasing mainland wolf populations caused considerable concern, as recorded in the annual reports, particularly among guides, hunters, and ranchers. Bounty payments, introduced at the turn of the century, were increased from $2.50 to $40 by 1948 (Preliminary Wolf Management Plan 1979[1], Min. of Environ., BC). There was a corresponding increase in the numbers of wolves taken by bounty hunters (Table 1). Although the species had no game or fur-bearer status within the Province, a considerable harvest of the wolf for fur occurred (Table 2). Royalties on pelts sold were temporarily introduced between 1920 and 1939 (PWMP).

The PWMP also refers to the establishment of a Predator Control Branch under the Provincial Game Commission in 1947. The use of poisons increasingly became the primary means of wolf control during the 1950s, particularly with the introduction of Compound 1080 (sodium fluoroacetate). Government personnel, ranchers, and guides distributed large baits on the ground and from aircraft in both livestock

Table 1
Numbers of wolves taken for bounty (1909–55) and control (1934–55)* (Wolf Management Plan 1979)

Year	No. of bounties paid	Year	No. of bounties paid	No. taken by branch in control 1934–55†
1909	655	1934	222	1
1910	581	1935	561	14
1911	467	1936	837	10
1913	277	1937	828	13
1914	382	1938	915	2
1915	299	1939	1159	n.a.
1916	210	1940	1659	25
1917	n.a.	1941	1002	30
1918	n.a.	1942	1039	8
1919	124	1943	1017	21
1920	84	1944	1321	27
1921	n.a.	1945	1202	26
1922	303	1946	932	26
1923	162	1947	1102	52‡
1924	195	1948	1156	66
1925	291	1949	1180	92
1926	336	1950	991	211
1927	344	1951	753	107
1928	452	1952	728	216§
1929	411	1953	544	207
1930	312	1954	415	113
1931	310	1955	202	60
1932–33	Bounty suspended			

*Taken from the 1955 Annual Report. In the mid-1970s about 200 animals were taken annually in control programs.
†No figures given from 1909–33.
‡Predatory-animal hunters hired for the Predator Control Branch, formed in 1947.
§The use of baiting stations expanded.

[1]Referred to subsequently as PWMP.

Table 2
Number of wolf pelts sold for fur, 1919–45*

Year	No. of pelts	Year	No. of pelts
1919	178	1933	446
1920	188	1934	841
1921	306	1935	837
1922	642	1936	828
1923	364	1937	915
1924	486	1938	1311
1925	215	1939	1349
1926	537	1940	167
1927	454	1941	169
1928	422	1942	943
1929	329	1943	1280
1930	363	1944	1157
1931	310	1945	71
1932	85		

Statistics Canada figures. Unavailable from 1946 to 1964.

management and wilderness areas. The program caused the species to become practically extinct in the northern and central livestock management areas by 1955 (1956 Provincial Game Commission rep.). Wolves were still plentiful in some wilderness areas, and the distribution of baits was extended to coastal inlets and offshore islands. Meanwhile, bounty hunting of the wolf was terminated in 1955.

Baiting ceased in wilderness areas in 1961, although a low-level control of the wolf continued in livestock and heavily hunted areas. However, the annual reports of the Game Commission described mounting concern over decreasing predator and increasing wild ungulate populations. The Predator Control Board was disbanded in 1963 (PWMP) and until 1973 predator management was administered regionally. In 1966 the wolf was given "big game", but not "fur-bearer", status, therefore trapping of the species was discontinued. In 1968 hunting of the wolf was closed on Vancouver Island and in southeastern BC, where the species was close to extinction. The PWMP describes a gradual establishment of protective bag limits (one to three) in most areas within the Province, designed to assist the recovery of the species in wilderness areas.

A non-resident trophy fee of $40 was introduced in 1970, and was changed into a $75 species licence fee additional to the $78 hunting licence (1980–81 Hunting Reg. Synopsis, Min. of Environ., BC). Wolves were given fur-bearer status in 1976 and trapping was opened during the 1976/77 winter in northern and central regions with high wolf populations (PWMP). The trapping season was extended during the 1980/81 season to northern Vancouver Island. The royalty paid on wolf pelts sold on the fur market was $2.28 in 1980/81 (1980–81 Trapping Synopsis, Min. of Environ., BC).

3. Current status

3.1. Classification

According to Cowan and Guiguet (1965) mainland BC is primarily inhabited by *C. l. columbianus* and Vancouver Island by *C. l. crassodon*; the subspecific and population status of *C. l. fuscus* in coastal mainland areas remains uncertain. An apparent recent invasion of eastern Vancouver Island by mainland wolves might have included members of the latter subspecies (I. Hatter, pers. comm.).

3.2. Distribution and abundance

Wolves occur at present throughout BC with the exception of the coastal and interior areas immediately north of the international boundary (Fig. 1) and the Queen Charlotte Islands. However, occasional wolf sightings have been made in the BC–Alberta–Montana border area in the southeast corner of the Province, raising hopes of the eventual re-establishment of a continuous wolf population from north to south in the Rocky Mountains.

Although accurate population figures are difficult to obtain, the wolf population has apparently recovered in all parts of the Province inhabited by them before the control programs in the 1950s. Based on local surveys, sight and track records, problem wildlife complaints, the extent of occupied area, and habitat availability, the provincial wolf population was estimated in 1979 as 6300 (PWMP). Moderate to high wolf populations occur in the north and central interior and in coastal areas, and low populations at higher elevations and within the southern parts of the wolf distribution range. Figures from selected mainland areas indicate a density range of 1 wolf/70–171 km^2 (PWMP). Particularly high local densities are reported from Vancouver Island, reaching 1/11.6–16.7 km^2 in one watershed under current study (D. Hebert *et al.* 1980, Fish and Wildl. Br., Min. of Environ., BC, unpubl. rep.).

4. Management

4.1. Objectives, strategies, and policies

The major objective of wolf management is to maintain viable wolf populations throughout BC where they are not in conflict with other land uses, e.g. established livestock-production areas. Wolf populations are allowed to fluctuate freely in response to changes in prey availability and other environmental conditions, and control will only be considered on a temporary and limited basis to prevent critical local declines in major prey species (PWMP). At present wolves are not controlled within the Province as a part of the protection of other wildlife species.[1]

4.2. Recreational hunting and trapping

The big game and fur-bearer status of wolves allows their controlled and restricted harvest within the Province. Seasons are open only during the fall and winter when pelts are marketable; there are no open seasons in areas where wolves are scarce. Bag limits are one to three, determined annually on the basis of relative wolf abundance within respective wildlife management areas. Year-round hunting and annual bag limits of 10 wolves are allowed only in some areas of chronic wolf problems and high wolf populations (1980–81 Hunting Reg. Synopsis, Min. of Environ., BC). There is no seasonal bag limit for trappers taking wolves.

With the exception of wolves shot by ranchers to protect their stock during the summer, most wolves taken by hunting and trapping show up on the fur market. During the past 16 years an average of 171 wolf pelts were sold for fur annually for an average of $15 354 per year (Table 3). Annual fluctuations in wolves taken reflect climatic changes affecting harvest, rather than market prices or changes in wolf populations (B. Saunders, Fish and Wildl. Br., Min. of Environ., pers. comm.). In addition, 2–4 dozen wolves are taken annually by

[1]Editor's note: wolf control to increase deer populations has since been carried out on Vancouver Island.

Figure 1
Wolf distribution in British Columbia

Figure 1

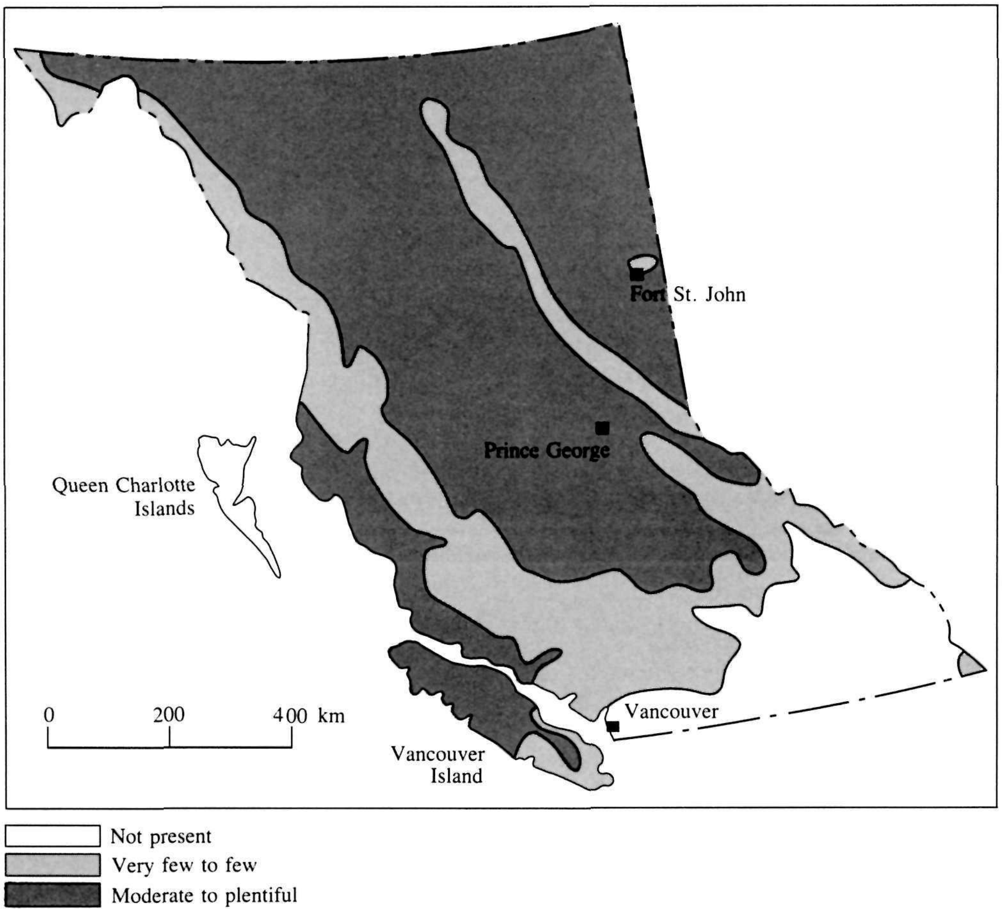


Table 3
Number and value of wolf pelts sold for fur, 1965–80*

Year	No. of pelts	Average price ($)	Total value ($)
1965	94	24.00	2 256
1966	102	16.98	1 732
1967	25	24.80	620
1968	54	41.83	2 259
1969	91	49.50	4 505
1970	39	49.55	1 932
1971	91	50.66	4 610
1972	265	57.26	15 174
1973	156	82.56	12 879
1974	117	84.88	9 931
1975	190	90.55	17 205
1976	151	116.45	17 584
1977	443	105.41	46 697
1978	406	145.79	59 191
1979	286	107.35	30 702
1980	228	80.65	18 388
Average	171	70.51	15 354

*Wolf Management Plan 1979; B. Saunders, pers. comm.

non-resident hunters for trophy (PWMP). The approximately 200–450 wolves harvested through recreational hunting and trapping represent 3–7% of the estimated provincial wolf population.

4.3. Areas of protection

Wolves have complete protection in all National Parks within the Province as well as in Wells Gray (5400 km^2) and Robson (2200 km^2) Provincial Parks. Robson Park is contiguous with extensive National Park areas in Alberta. None of the National Parks within BC are considered large enough to provide sanctuary for self-sustaining wolf populations (L. Carbyn, pers. comm.).

5. Research activities

5.1. Vancouver Island projects

A graduate student program sponsored by the Fish and Wildlife Branch focused on the food habits and social organization of the Vancouver Island wolf, *C. l. crassodon*, in a 530-km^2 area west of Kelsey Bay (Scott 1979, Scott and Shackleton 1980). A further student program, in the same general area of Vancouver Island, was set up to study wolf predation on black-tailed deer fawns and is now near completion (I. Hatter, pers. comm.).

5.2. Wolf–caribou study

A 3-year study of wolf–caribou interaction by Fish and Wildlife Branch personnel was completed in BC in 1981 (D. Eastman 1981, Fish and Wildl. Br., Min. of Environ., BC, unpubl. rep.). They paid particular attention to wolf-related woodland caribou (*Rangifer tarandus*) calf mortality. The project dealt with two separate areas in northern BC that had approximately identical ecology, Level Mountains and Horseranch Range. The former area was used for test control. In the latter area they removed approximately 24 wolves during each of three consecutive winters (1978, 1979, and 1980) to test changes in caribou calf survival.

5.3. Wolf–livestock study

Wolf–livestock interaction was studied by Fish and Wildlife Branch personnel, with rancher co-operation, in the Bulkley Valley during two consecutive grazing seasons (1979 and 1980). The project was designed to provide information on wolf-related cattle mortality on remote summer ranges and on the influence of

Figure 2
Wolf–livestock conflict areas in British Columbia, 1978–81

husbandry practices on wolf predation (D. Hatler 1981, Fish and Wildl. Br., Min. of Environ., BC, unpubl. rep.).

Data on problem wolf management in the Province were analysed and evaluated to assist future program planning and to provide a better understanding of cause–effect relationship in wolf conflict situations (Tompa, this publication).

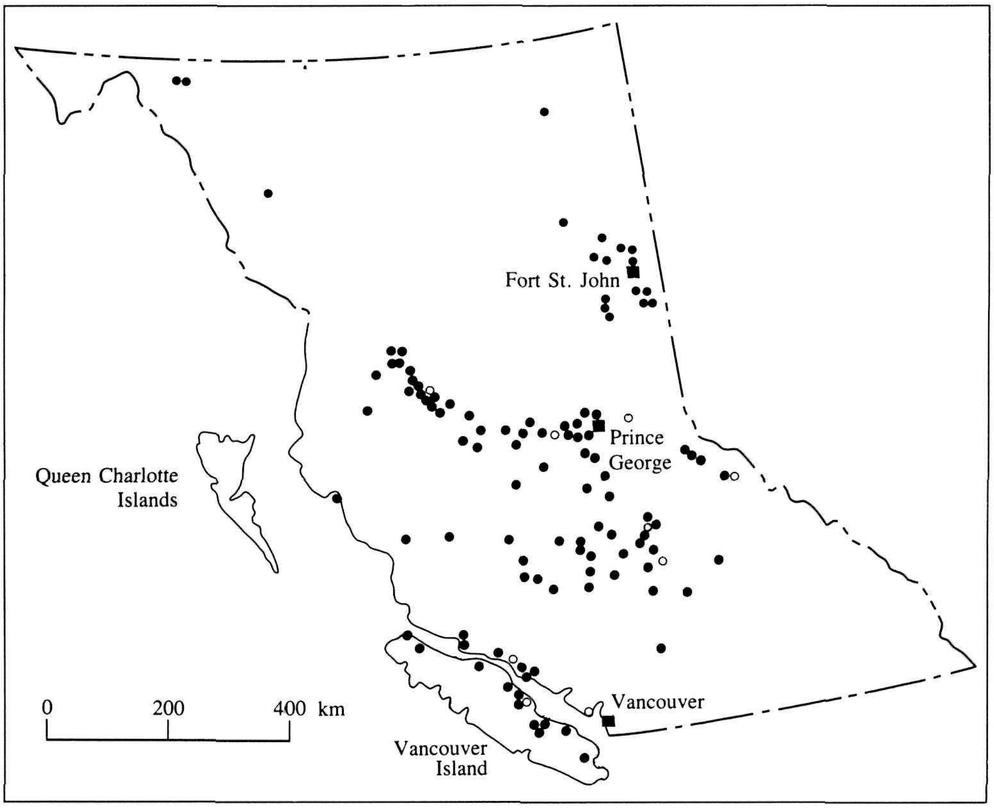
6. Problem wolf management

6.1. Distribution of wolf conflicts

The majority of wolf–human conflicts relate to attacks on domestic animals, although an increasing number of human safety related problems were reported during 1979, 1980, and 1981. Most complaints are received from livestock ranges and rural settlements situated in the central interior of the Province and along the east coast of Vancouver Island. Between January 1978 and March 1981, on the basis of verified complaints, 117 wolf conflict areas were recognized (Fig. 2). In 9 of these areas problems were caused by single wolves only, in the remaining 108 by pairs or packs (Tompa, this publication).

Wolves were responsible for livestock losses valued at over $65 000 a year between 1978 and 1980 (Tompa, this publication). Although this level of loss does not threaten the livestock industry, losses to individual farmers can be considerable.

Figure 2



• **Packs and pairs (N = 108)**
○ **Single wolf conflicts (N = 9)**

6.2. Policies and procedures

Under existing policies (Ministerial Directives on Problem Predator Management 1979, Min. of Environ., BC, unpubl.) wolves that kill, maul, or harass domestic animals, or cause concern for human safety are controlled on a reactive, site-specific basis. Complaints are investigated by trained Ministry personnel before any management action is taken. Where faulty husbandry practices are directly responsible for wolf conflicts, control is refused and improved husbandry is recommended. The Ministry does not guarantee a predator problem-free situation, and is not financially or legally responsible for damage caused by wildlife.

In 1974/75 a Provincial and a series of Regional Problem Wildlife Management Advisory Committees were established to advise the government, assist in policy development, and help management program planning and implementation. The committees include representatives of the Ministries of Agriculture and Food and of Environment, and of important producer and conservationist organizations within the Province. The committees have had a major role in the development of current policies and programs for problem wolf management.

6.3. Control methods

Before 1979 the primary approach to wolf conflicts was to control them on a site-specific basis through the use of poison baits (strychnine, cyanides, and Compound 1080). Small baits were placed to remove individual problem animals and large baits were used to reduce local population levels or control a problem pack. Preventive baiting was applied in areas of confirmed wolf-related livestock losses in late winter programs, prior to livestock reproductive periods.

A moratorium on poison baits was declared in December 1978. During the moratorium, the primary means of control was by aerial hunting by appointed Ministry personnel. The moratorium was lifted in June 1979 by the Minister of Environment; poison baits were again applied after July 1980, when a pesticide use permit, allowing the use of Compound 1080 baits by certified Ministry personnel, went into effect (Tompa, this publication).

Poison baits can now only be used in situations where shooting or trapping would not resolve the wolf conflicts (Ministerial Directives on Problem Predator Management 1979, Min. of Environ., BC, unpubl.). Shooting on the ground generally depends on a chance witnessing of a wolf attack on livestock — a rare occurrence. Aerial shooting has only limited and local significance during the winter at times when wolf-related livestock losses are low. The method is expensive (up to $2000/wolf) and the probability of taking wolves not involved in conflict situations appears to be high (Tompa, this publication).

Trapping has not been a very successful method of wolf control, partly because of the lack of experienced wolf trappers within the Province, particularly within livestock production areas. Increased emphasis is currently placed on the use of leg-hold traps and killing snares in response to specific needs.

Although the ground shooting and trapping of problem predators by livestock owners is legal under provisions of the 1979 Wildlife Act, the pesticide use permit issued to the Fish and Wildlife Branch under the 1979 Pesticide Control Act restricts the use of Compound 1080 baits to certified Ministry personnel. The permit (Pesticide Use Permit 125-15-80:85, Pesticide Control Branch 1980, Min. of Environ., BC) severely restricts the use of Compound 1080 baits in order to maximize public and environmental safety and to prevent a harmful impact on wilderness wolf populations. Poison baits are not allowed in wilderness control programs (none are in progress at present). A maximum of 250 individual wolf baits may be used annually. The quantity of Compound 1080 in the baits (13 mg) is calculated to kill one wolf and to minimize the chances of non-target poisoning. A maximum of 12 individual baits may be placed at the site of a confirmed wolf attack. The baits are buried in the ground or under snow cover and a draw bait or attractant scent is applied. Baits not taken must be removed after a period of 2 weeks.

Although the carcasses of wolves killed by Compound 1080 baits are difficult to locate, there is no indication that the method is less effective in resolving local wolf-related problems than other lethal control methods (Tompa, this publication). In spite of the absence of visible results of control actions, Compound 1080 is preferred to strychnine and cyanide products because of the greatly reduced human and environmental safety hazards (Tompa, Pesticide Rev. 1979, unpubl. rep.). From the reintroduction of Compound 1080 into control programs in July 1980, up to May 1981, 47% ($N = 149$) of 320 wolf baits placed were taken by wolves and 17% ($N = 54$) by non-target species, including 28 coyotes (9%).

During 1978, 1979, and 1980 the numbers of problem wolves removed by control were 186, 56, and 138 respectively (Tompa, this publication) representing 1–3% of the provincial wolf population. The figures express a maximum rather than an absolute control impact, as they include wolves suspected dead in the absence of a carcass after they had taken poison baits. There is no indication anywhere within the Province of wolf population declines as a result of control activities under the existing policies.

When available, beaver are important prey items for wolves (photo: CWS)

Status and management of wolves in Alberta

John R. Gunson

1. Abstract

Population history and management of the wolf during the past 200 years in Alberta are reviewed. Two major declines in abundance occurred between 1880 and 1920 and between 1952 and 1956; both were related to human control. An estimated 5000 wolves currently occupy approximately 404 000 km^2 in Alberta, including most of the "Green"[1] area and portions of the settled areas. Area of total protection in three National Parks and three provincial Wilderness Areas is 19 053 km^2 (about 3% of Alberta). Wolf control in the 1970s was limited to areas of livestock depredations; less than 2% of the provincial population was removed annually. Population and biological studies are summarized.

2. Range and numbers

2.1. Historical

In 1754, somewhere in what was to become the Saskatchewan–Alberta border area, Anthony Henday, the first "white man" to explore central Alberta, wrote in his diary "Wolves without number", and later recorded "I cannot say whether them [wolves] or the Buffalo are most numerous" (Burpee 1907). These observations reflected the abundance of wolves (*Canis lupus*) associated with the larger ungulates, especially bison (*Bison bison*), of the northern prairies before and during exploration and the early fur trade. Many of the later historical observations and management programs concerning wolves in Alberta were reviewed by Stelfox (1969), Nowak (1974, unpubl. rep. New York Zool. Soc. and US Bur. Sport Fish. Wildl.), Carbyn (1974) and Mattson and Ream (1980, Univ. Montana, unpubl. rep.).

David Thompson observed wolves in the Athabasca Valley [now Jasper National Park (JNP)] in 1810 (Carbyn 1974) and Alexander Henry observed many wolves in the foothills west of Rocky Mountain House in 1811 (Coues 1897). The Palliser expedition of 1857–60 (Spry 1963) reported wolves were plentiful throughout the prairies and foothills, noted exceptional abundance of wolves in the Battle River area, and recorded the native Indian reports of occasional rabies epizootics in wolves. McDougall (1898) reported wolves were very numerous around bison hunting camps in 1865 and were killing Indian horses.

Wolves were abundant in the prairies and foothills of what was to be Alberta until at least the 1870s. They also occurred in the mountains and northern forests, but probably at lower densities. During the 1860s and 1870s bison herds were systematically eliminated for their hides and meat. Other native ungulates were greatly reduced by hunters supplying mining camps and towns and possibly by very severe winter weather, while wolves were poisoned for their pelts and in retaliation for raids on meat caches. "Wolfing" — strychnine poisoning of wolves on bison carcasses — became an easy and lucrative means of taking wolves (Rodney 1969). Beef cattle were driven north from the western United States during the 1870s and 1880s and wolf predation on cattle was recorded as early as 1885 (McCowan 1950), especially in the foothills regions where wolves remained more common. By 1890 the bison were virtually eliminated, cattle were common, and wolves were drastically reduced in numbers in the prairie portion of "Alberta". A wolf bounty was established in 1899 (Pimlott 1961).

Stelfox (1969) estimated that wolves were very scarce along the eastern slopes of the Rockies and practically non-existent in the Prairies and parklands of the central portion of the province by 1900, although Williams (1946) reported two wolves with young near Milk River and others in extreme southern Alberta during 1923–25. Stelfox further noted observations of declining wolf abundance in northern Alberta between 1900 and 1930. This decline in numbers in the western and northern boreal forests was probably related in large measure to the use of strychnine during winter months by trappers of that period, to trapping, and to the decline in numbers of large ungulates, especially elk (*Cervus elaphus*)(Millar 1915, Cowan 1947).

Soper (1964) reported wolves in Wood Buffalo National Park (WBNP) in 1925 and a southwesterly (and perhaps easterly from British Columbia) expansion of range and numbers apparently occurred throughout the 1930s and 1940s. Wolves were reported south of Grande Prairie by the mid-1930s (Stelfox 1969), were common north of the Athabasca River by 1939 (Soper 1964), and occupied the vicinity of JNP in the 1930s (Anderson 1938, Can. Wildl. Serv. Rep., Ottawa, Ont.; Clarke 1942, Can. Wildl. Serv. Rep. CWSC.810, Ottawa, Ont.; Stelfox 1969). Farther south, wolves reached Banff National Park (BNP) in 1943 (Green 1951) and lone individuals reappeared in Waterton National Park (WNP) in the extreme southwestern corner of the Province in 1943 following extermination there in 1922 because of livestock depredations (Cowan 1947).

With the return of wolf abundance in northern and western regions, concern for the welfare of game animals soon followed (Callison 1948). During the 1940s and 1950s wolves were reduced in JNP as part of the management of ungulates and to help control rabies (Cowan 1947, Carbyn 1974). Numbers were also reduced in WBNP in 1941–42, 1948–49, 1951–52 (Fuller and Novakowski 1955) and the reductions continued for the years 1952–53, 1953–54, 1957–58, and 1959–60 (L. Carbyn, pers. comm.). Soper (1948) reported severe wolf depredations on livestock in the Peace River region. Stelfox (1969) thought the continued build-up in wolf numbers was related to light trapping during the war years (1939–45) and to expanding numbers of native ungulate prey. However, harvests of wolves were relatively high during the war years (Todd and Geisbrecht 1979), but trapping intensity was low during the late 1940s and early 1950s.

2.2. Rabies control (1952–56)

In June 1952, rabies was reported in red fox (*Vulpes vulpes*) in northeastern Alberta, a spread of the infection from extremely high-density fox populations in adjacent Northwest Territories. By February 1953 the disease had spread to coyotes (*Canis latrans*) in southern Alberta and to many other wild and domestic species (Ballantyne and O'Donoghue 1954). One wolf was laboratory-diagnosed as rabid and several other rabid wolves harassed residents and transmitted the disease to swine and cattle, all in the Fort Vermilion area of northwestern

[1]Special land designation for Alberta.

Wolf-poisoning programs can eliminate entire packs. These wolves were poisoned in the 1960s on a lake adjacent to Prince Albert National Park, Saskatchewan (photo: L.N. Carbyn)

Alberta (Ballantyne 1957, Alberta Agric., unpubl. rep.). Traplines to control carnivores were established along fringe agricultural–forest areas and in the vicinity of some northern communities. During 1952–56 an estimated 5461 wolves were removed by strychnine poisoning, snaring, trapping, and denning (Ballantyne 1958). Stelfox (1969) estimated 90% of the kill was in northwestern Alberta; he considered the provincial population in 1952 to be 5000 and during 1956–60 to be between 500 and 1000 wolves.

2.3. Population and range expansion (1957–76)

Whereas during 1952–56 wolf control was primarily intended to reduce populations of rabies vectors, control during 1957–66 continued for reasons related to ungulate management, although at reduced vigour. On provincial lands attempts were made to integrate wolf control with big game numbers, range conditions, wolf populations, hunter harvests, and distributions (Stelfox 1958, Alberta Fish and Wildl. Div., unpubl. rep.). Distributions and estimated numbers of wolves were reported and wolf control was recommended for certain areas (Stelfox 1964, 1965, Alberta Fish and Wildl. Div., unpubl. rep.). Wolf control in National Parks in Alberta ceased in 1959 (Carbyn 1974).

Wolves continued to increase in numbers throughout this period; Stelfox (1969) estimated 3550 wolves in 1965–66. By 1966 wolves occupied permanent territories to at least the Bow River west of Calgary, and lone individuals were reported as far south as Pincher Creek and near WNP (Stelfox 1969). By 1970 wolves occurred farther south in the Highwood River area, and by 1976 wolves were reported killing cattle near the south end of the Livingstone Range. A lone wolf was shot near the Cypress Hills in the southeastern corner of the Province in 1971.

By 1966 wolf control, as part of big game management, was phased out, but occasional wolf control continued in response to livestock depredations. By 1972 wolf–livestock depredation complaints had become more common and annual control was initiated (Gunson 1973, Alberta Fish and Wildl. Div., unpubl. rep.).

Figure 1
Range and areas of total protection of *Canis lupus* in Alberta in 1981

2.4. Current (1977–81)

Numbers of wolves have probably stabilized throughout most of the Province during recent years. Wolves have reoccupied small forested portions of the settled areas (Fig. 1). Depredations of livestock occur annually in these areas and on grazing leases in adjacent portions of forested public lands. Total occupied range in 1981 was 404 000 km^2. Estimates from studies in three areas (Fort McMurray, Swan Hills, and Simonette River), when projected over the whole Province, provide a population of 4000 at a mean density of 1 wolf/101 km^2 (Fuller and Keith 1980; Bjorge and Gunson, this publication). However, the populations in two of these areas had been reduced by trapping and poisoning, and in the third, Fort McMurray (1 wolf/151 km^2), the population was limited by the low numbers of ungulates. Hence the provincial population may be somewhat greater than these estimates indicate, perhaps 5000 wolves.

The southerly expansion of range along the western mountains and foothills during 1957–76 did not continue during the 1977–81 period. The most southerly range occupied by reproductively active wolves appears to be the northwest branch of the Oldman River, where at least one pack had been reported during 1977–79 (Mattson and Ream 1980, Univ. Montana, unpubl. rep.).

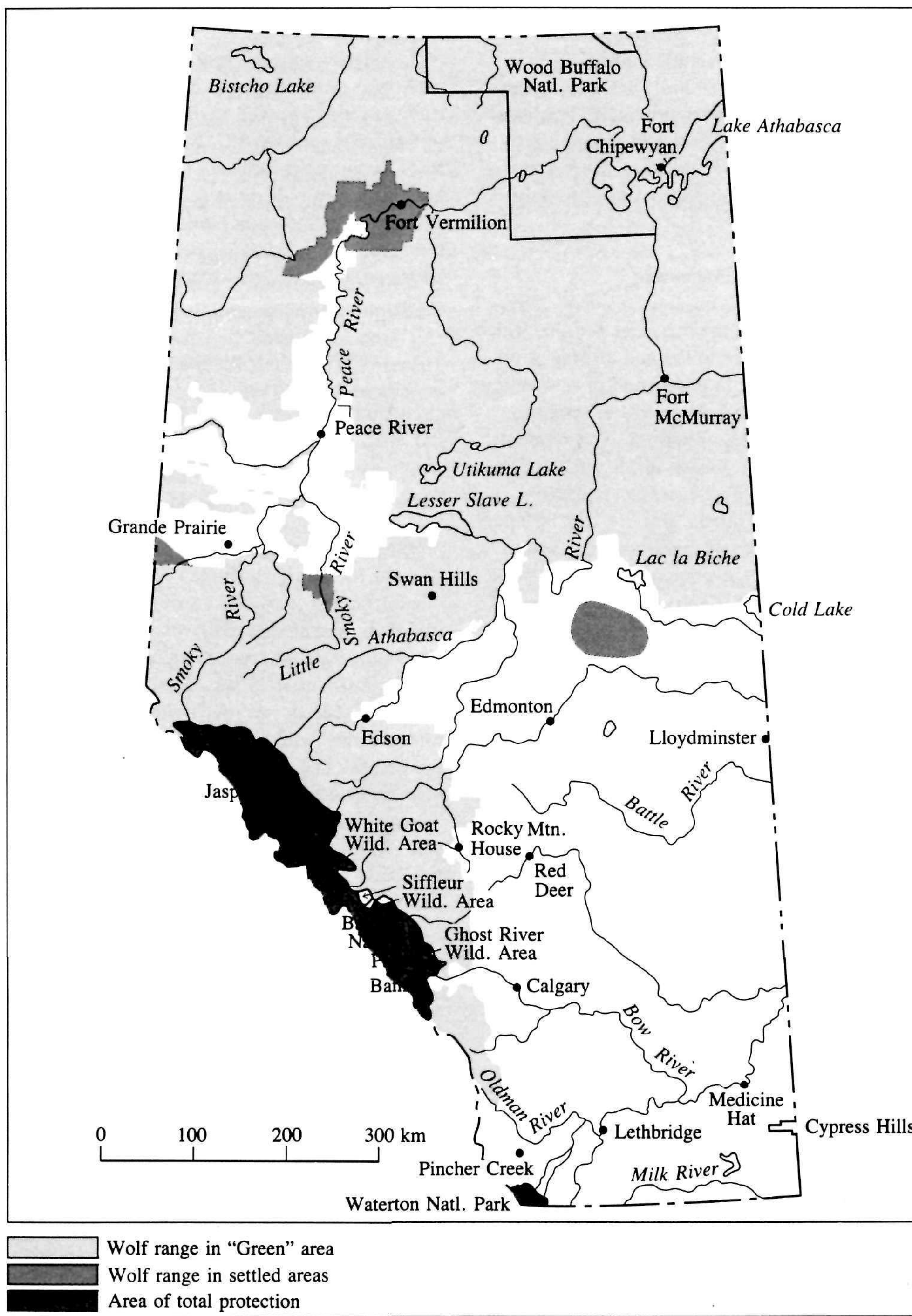
3. Regulations and policy

Bounties were paid on wolves in Alberta between 1899 (Pimlott 1961) and 1954 (see Todd and Geisbrecht 1979 for a review of bounty values).

Since 1964 wolves, together with coyotes and wolverine (*Gulo gulo*), have been classified as "fur-bearing carnivores" (Wild Fur Industry Reg's. 356/79, Sec. 2) because of their potential predatious behaviour. Residents may shoot a wolf on most deeded lands without a licence and during all periods of the year.

Since the late 1960s the policy in regard to ungulate management has been that predators could be removed only if the mortality they caused was suppressing prey numbers. Such predator control of wolves has not been conducted since 1966, although ungulate–predator

Figure 1



relationships have not been adequately documented in most areas.

Total protection is afforded the wolf in three of the four National Parks (BNP, 6641 km^2; JNP, 10 878 km^2; WNP, 526 km^2) and in three mountainous provincial Wilderness Areas (total 1008 km^2). Native trapping is allowed in remote WBNP. Area of total protection is 19 053 km^2, or approximately 3% of Alberta.

4. Hunting management

In most forested areas residents may shoot a wolf during the big game season, which lasts from September to the end of May. Currently they must be in possession of a wildlife certificate, although before 1981 a valid big game licence was also required. Non-residents may hunt wolves in season under the authority of a Non-resident Wolf Licence. Because wolves are wary animals, few are shot by hunters. The wolf is considered by some a prized trophy animal yet the price of the Non-resident Alien Wolf Licence ($150) has discouraged such harvest (D. Simpson, pers. comm.). Hunting from aircraft is not permitted.

5. Fur management

The first governmental recognition of the wolf as a furbearer in Alberta was 1967, when a regulated season (1 September – 30 April) was established for registered trappers (public lands) and for resident trappers (settled, deeded lands). The trapping season was lengthened to 1 September – 31 May in 1976 but currently runs from 1 October to the end of February. Trapping methods permitted are snares, traps, and shooting on registered traplines, and traps and shooting on resident trapping areas.

Fur harvests vary considerably from year to year. Records indicate a peak in the numbers of wolf pelts (2129) marketed in the province in 1922–23 (Todd and Geisbrecht 1979); many of these pelts were probably taken in the NWT and the bounty claimed in Alberta (as stated earlier, numbers of wolves in Alberta were low during that period). Production of pelts was low during 1947–54 (less than 100 in most years), a result of low pelt prices, but harvests have not increased significantly during 1966–80 despite sharp price increases resulting from the demand for long-haired fur (Todd and Geisbrecht 1979).

During the 10-year period 1971–80 mean pelt production was 532 (range 177–880). Raw pelt value peaked in 1978/79, when a total of 541 pelts sold for $67 246, i.e. an average of $124.30 per pelt. Skilled wolf trappers have been scarce in Alberta in recent years despite substantial increases in pelt value. Programs to train wolf trappers are needed, especially in fringe agricultural areas where depredations occur.

6. Depredation management.

During 8 years (1972–80) 1077 wolf complaints were registered with Fish and Wildlife offices in Alberta. Depredations on cattle, sheep, swine, goats, horses, dogs, and poultry were reported. Complaints are investigated by District Fish and Wildlife officers or regional problem wildlife specialists. Wolf control is carried out following confirmed or highly probable documentation (Roy and Dorrance 1976) of livestock predation, usually by placement of strychnine baits in specific areas of depredations (Gurba and Neave 1979). Control is only partially site-specific, as much wolf removal continues during winter, several months after depredations. The policy is to conduct control operations to a maximum of 19 km into the "Green" area (1981, Alta. Energy and Nat. Resour. Map), including those complaints where predation has occurred on grazing leases on public lands.

Seven hundred wolves were removed during 1972–80, a mean of 88 per year or less than 2% of the provincial population. Alternative methods of removing offending wolves are required because strychnine poisoning, although effective, is not sufficiently selective or humane.

Alberta Agriculture initiated a predator indemnity program in 1974 to compensate ranchers for losses of livestock (food-producing animals only) to predators. Compensation is at 80 or 50% of losses judged to be confirmed or probable, respectively. Standard livestock values, reflecting the market, are determined annually. Claims are reviewed by either a Peace River or Southern Committee. Committees are composed of representatives from the Department of Agriculture, Fish and Wildlife Division, together with a veterinarian and producers. During 1974–80, 384 wolf-livestock claims were approved (Gunson, this publication).

7. Demographic and biological studies

Cowan (1947) studied the wolves of the Rocky Mountain National Parks during 1943–46. He determined a very low wolf density of 1 wolf/225–287 km^2 in JNP, an area of abundant and diverse prey. Elk was the most frequent prey (47% occurrence in scats), although a wide variety of large ungulates were utilized and mule deer (*Odocoileus hemionus*) were selectively hunted. According to Cowan (1947) wolves were not controlling ungulates, which were high in number during that period. He identified sarcoptic mange as a serious mortality agent, especially on pups (see Green 1951 and Todd *et al.* 1981). Rowan (1950) reported the range occupied by a pack of eight wolves in the Clearwater River area in 1944–45. Green (1951) summarized wolf observations in BNP between 1931 and 1950. He stated that re-establishment of wolves occurred in the 1940s, with first observations in 1943. His notes include data on physical characteristics, behaviour, movements, litter size, prey utilization, and occurrence of mange.

Fuller and Novakowski (1955) reported results of 59 wolves taken in WBNP in 1951–52. They found that bison (*Bison bison*) was the major winter prey, and Fuller (1962) elaborated on this. Their other observations included incidence of parasitism, reproduction, sex and age, behaviour at baits, and movements. They were the first to report high juvenile mortality in an unexploited wolf population.

Stelfox (1969) reviewed the demographic status of the wolf in Alberta between 1800 and 1969. Francis (1960) reported two observations of wolves by wardens in BNP. Kemp (1966, Alberta Fish and Wildl. Div., unpubl. rep.) summarized sex, age, and measurements of 30 wolves taken in northeastern Alberta.

Carbyn (1974, 1975*a*) recorded the history of the wolf in JNP and studied wolf–ungulate ecology. His observations reaffirmed

Cowan's findings of dependency on elk, especially calves, and mule deer. Wolves were observed at dens and at rendezvous sites. Despite an abundance of ungulate prey, lick sites were not heavily utilized by wolves to kill prey (Carbyn 1975*b*).

Fuller and Keith (1980) used telemetry to study wolf populations and predation in the Swan Hills and Fort McMurray areas of central and northeastern Alberta during 1975–78, the first time this technique had been used on wolves in Alberta. Wolves in the Fort McMurray area were at a fairly low density (1 wolf/151 km^2) as were their principal prey, moose (*Alces alces*). A higher density was observed in Swan Hills (1 wolf/83 km^2) where moose were about eight times as common as in the Fort McMurray area. Wolves were considered the major cause for the declining (at best stationary) moose population in the Fort McMurray area.

Studies of wolf predation on cattle were conducted on remote grazing leases along the Simonette River in northwestern Alberta during 1976–81 (Bjorge 1980; Bjorge and Gunson, this publication). Wild ungulates (four species) formed the bulk of wolves' diet during both winter and summer. During the grazing season, however, cattle became an important secondary constituent of the diet, some of it acquired by scavenging. Lone wolves were more dependent on cattle than were packs.

During 1972–80, 639 wolves taken during governmental control were necropsied. Biometrics, abnormalities, disease, reproduction, sex, and age were recorded (Myers and Gunson 1979, Alberta Fish and and Wildl. Div., unpubl. rep.) and computerized. Records of skull size (Gunson and Nowak 1979) and papillomatosis (Samuel *et al.* 1978), trichinosis (Gunson and Dies 1980), and mange (Todd *et al.* 1981) are published.

A movement of 670 km made by a wolf from the NWT through northern Alberta was recorded in 1977 (Van Camp and Gluckie 1979). Oosenbrug and Carbyn (1982) reported preliminary (1978–79) results of a study of wolves and wolf–bison predation in WBNP. Field work was completed in 1981 and reports for Parks Canada are in preparation.

8. Taxonomy

Cowan (1954) reported that *Canis dirus* occurred in western Alberta during the Pleistocene. Goldman (1944) and Hall and Kelson (1959) listed five subspecies of wolves in Alberta in historic times, although Jolicoeur (1959), Nowak (this publication) and others have questioned the degree of subspeciation in western Canada. Skeel and Carbyn (1977) noted little affinity between northern and southern samples in western Canada. Extensive reductions of wolves in Alberta noted earlier would very probably have altered subpopulation differences, mostly to the advantage of more northern types. Two types found in southern Alberta, *C. l. irremotus* and *C. l. nubilus* were probably eliminated.

9. Acknowledgements

I thank L.N. Carbyn, G.B. Kolenosky, and J.G. Stelfox for their reviews.

Status and management of wolves in Manitoba

Richard R.P. Stardom

1. Abstract

Conflicts between humans and wolves occur in almost every situation where man has attempted to occupy traditional wolf range and Manitoba is no exception. Since the arrival of Europeans in the Province during the early 1600s wolf populations have gradually been reduced to a remnant of their former numbers by loss of habitat and prey, fur harvests, and control programs. The current provincial wolf population is considered to be relatively stable at approximately 4000 animals. Wolves are classified as big game and can be hunted or trapped during specified seasons. On private land they may be killed at any time in defence of property. Total protection is afforded only in Riding Mountain National Park, an area of 2944 km^2.

Over the past 10 years the average annual harvest has been 356 pelts, with an average annual value of $31 760. These figures do not include the unknown number of wolves taken in control programs or for property protection, or pelts kept for personal use. In 1980/81 the harvest was 422 pelts with a total auction value of $39 246. The long-term potential annual harvest is estimated to be 400 pelts.

Wolf control is reactive and area specific. Methods are primarily limited to the use of cyanide guns, snares, and strychnine baits. Control programs may be implemented in response to livestock depredation or complaints from remote communities. No wolf control programs are being carried out at present to increase prey populations. No compensation payments are made for livestock killed or injured by wolves.

2. Historical overview

Before the arrival of the first Europeans in Manitoba, wolf (*Canis lupus*) populations presumably existed in much larger numbers than now. An abundance of prey, particularly bison (*Bison bison*), barrenground caribou (*Rangifer tarandus groenlandicus*), and woodland caribou (*Rangifer tarandus caribou*), provided a basis for the Province-wide distribution of large numbers of wolves. Harvesting of wolves would also have been minimal, as some cultures (e.g. Swampy Cree) regarded wolves as kindred spirits (W. R. Burns, pers. comm.) and there was no great demand by the natives for wolf skins as clothing. As primitive hunters, the natives probably competed with wolves for the same prey on an almost equal basis (Pimlott 1967*a*).

The onset of the fur trade in Manitoba with the arrival of Thomas Button in Hudson Bay in 1612 (Rich 1967) started the eventual reduction in wolf populations. The superficial nature of the fur trade during the first 100 years after the trading posts were set up probably had a minimal effect on wolf populations, as few traders ventured inland and the European demand was primarily for beaver (*Castor canadensis*). As posts were set up inland during the 18th century and settlers encroached on wolf habitat during the early 19th century, increasing human/wolf contact resulted in wolves being killed either for their fur or as a predator control measure. In fact, some early attempts at cattle herding failed because of losses from wolves and the cold (Morton 1957).

During the 19th century, increasing numbers of European settlers, with fear of wolves as part of their culture, continued the destruction of wolf populations in southern Manitoba, using improved guns and steel traps. Protection of livestock necessitated killing of predators, and cultivation of the land and urbanization removed traditional wolf habitat. Competition for big game and elimination of bison by the 1870s considerably reduced the availability of prey for wolves, particularly in southern Manitoba.

During the 1920s and particularly during the Depression of the 1930s, large numbers of trappers moved northward in the Province (Carmichael 1973, Man. Dep. of Mines, Resour. and Environ. Manage., unpubl. rep.) and effected wolf reductions even in remote areas. The killing of wolves during this period may not have been specifically for the pelt but a manifestation of the fear and hatred felt for wolves. The introduction of the Registered Trapline system during the 1940s and early 1950s reduced the number of trappers and removed many of the efficient profit-motivated trappers from remote areas. This probably resulted in fewer wolves being taken.

Concerns for the effects of wolves on big game species resulted in an extensive predator control program which began about 1950 (Emberley 1968, Man. Dep. of Mines, Resour. and Environ. Manage., unpubl. rep.). In an attempt to reduce wolf populations, large numbers of poison baits were set out throughout much of the wolf range in the Province. Changing wildlife philosophies and the questionable benefits of wolf control caused the termination of the program in 1965. Increased ecological awareness has rationalized the attitudes and approach of both public and government toward wolves and wolf management (Theberge 1977). Wolf populations have now stabilized at numbers presumably lower than those of 350 years ago, but consistent with the 17% loss of original range and the reduction in prey.

3. Current distribution and abundance

The current provincial wolf population is considered stable at approximately 4000 animals. Their distribution covers most of the forested areas of the Province (Fig. 1), with abundance primarily dependent on the available prey and harvest pressure. Wolf densities considered to be as high as 1 wolf/15–20 km^2 are distributed along the taiga east of Lake Winnipeg and extend across the northern Interlake to the Grass River drainage system. From this crescent, wolf numbers diminish northward beyond the continuous forest and southward and westward toward the aspen parkland and the agricultural areas.

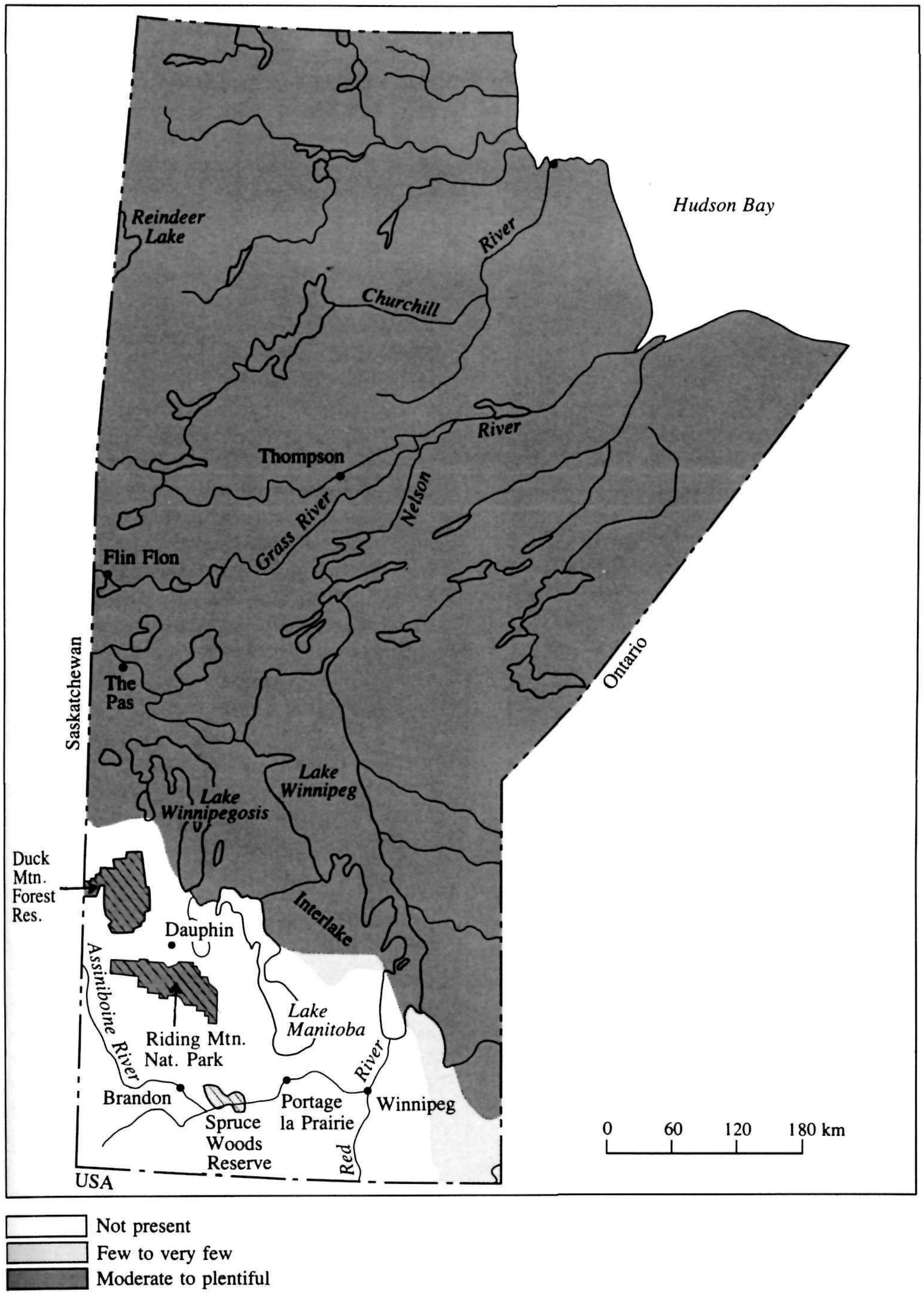
Island forests such as the Shilo Military Reserve/Spruce Woods Provincial Park (405 km^2), Riding Mountain National Park (2944 km^2), and Duck Mountain Provincial Park/Forest Reserve (2290 km^2) support low to moderate densities of wolves. Scattered individual wolves and unstable packs exist in the southeastern corner of the Province, the central Interlake, and in The Pas area. Wolves in the last two areas are subject to intensive trapper harvest and to occasional control measures related to livestock depredation.

4. Protection and control

Wolves are completely protected within Riding Mountain National Park (Fig. 2). They are not protected, however, when they travel out of the park into the surrounding agricultural

Figure 1
Wolf distribution and abundance in Manitoba

Figure 1



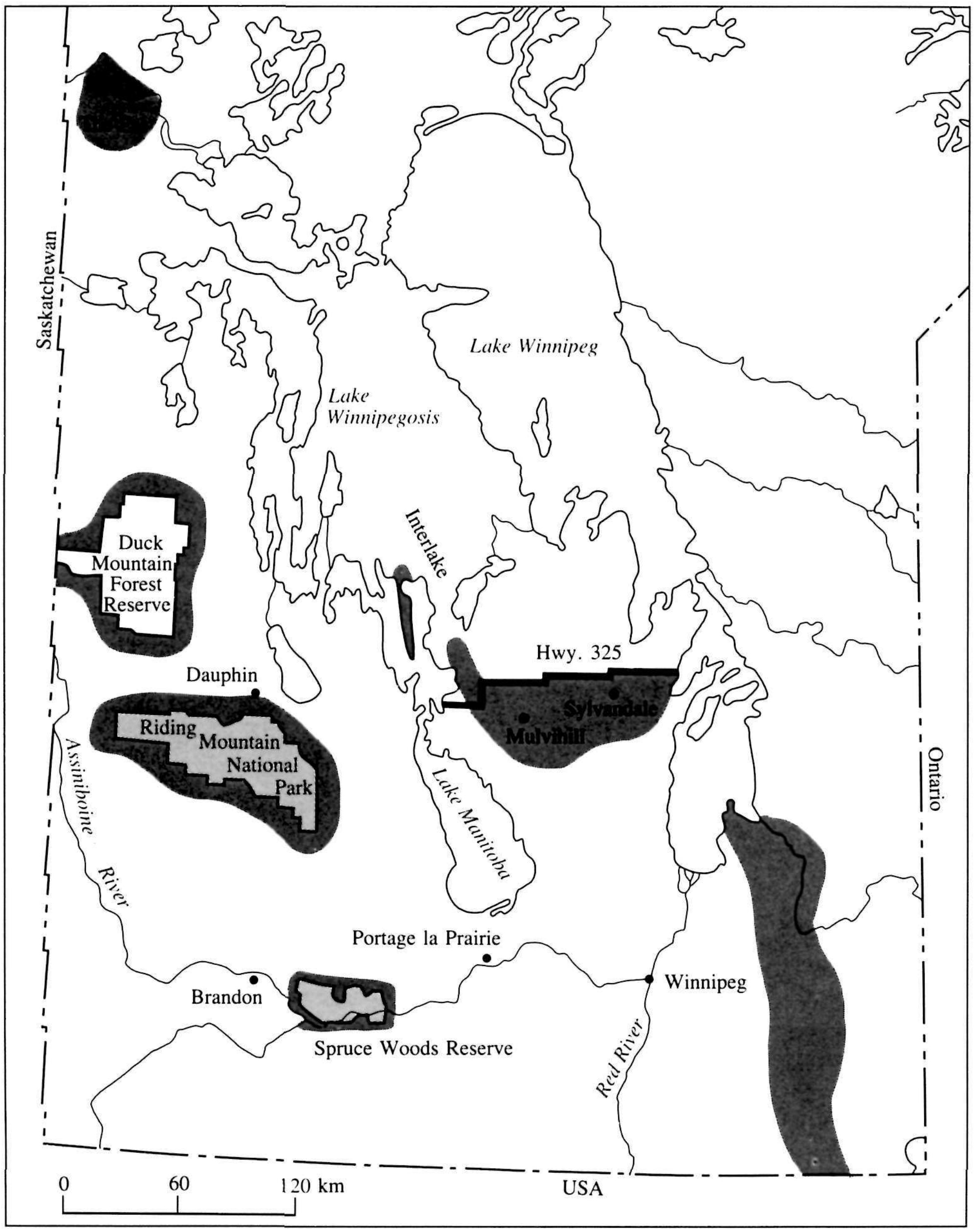
areas and several are taken each year (Carbyn 1980, unpubl. final report; Carbyn 1981). The park is considered barely large enough to sustain a viable wolf population. Partial protection is provided for the few individual wolves in the Shilo Military Reserve and the Spruce Woods Provincial Park only by the specific restrictions on hunting and trapping in these two areas. Although the potential for wolf–livestock interactions exists along the periphery of these areas, as well as around the Duck Mountains and along the western edge of the southeastern wolf range, few complaints are voiced by resident livestock owners. Occasional complaints have been made in The Pas area but the chronic complaint area is the central Interlake, which has been a wolf–livestock problem area for over 20 years. On occasions in the past, wolf populations have been severely reduced in the area south of highway 325, but re-invasion and recruitment by wolves from the area immediately to the north is rapid. Two major Community Pastures, Mulvihill and Sylvandale, were established within this traditional wolf range and additional problems are created by ranging cattle on forested and semi-forested leased Crown land, often far removed from the livestock-owner's residence (Hill 1979). A relatively low prey base exists across portions of the area, which further complicates the situation. Following control programs in 1979 and early 1980, which removed 11 wolves, there were no complaints during the 1980 range season.

5. Economics

Wolves are not a major component of total fur production value for the Province but they do provide a constancy of supply over the long term (Fig. 3). This supply of wolves in relation to the actual population is considerably more stable than is indicated by fur production records, which in early years included "brush wolves" or coyotes (*Canis latrans*). An administrative shift in recording provincial harvest figures from the Dominion Bureau of Statistics to the Province of Manitoba occurred in 1944, about the time of Registered Trapline implementation. Average pelt values indicate no

Figure 2
Areas where wolves are protected, and regions of potential wolf–livestock problems in southern Manitoba

Figure 2



Protected areas
Potential wolf–livestock problem areas

major change resulted from the recording shift, supporting the federal Bureau's data.

Average annual harvest over the past 10 years has been 356 pelts, with an average annual value of $31 760. In 1980/81, 422 wolf pelts were sold through the fur market for a total auction value of $39 246. It must be recognized that for the most part these are "new" dollars injected into the economy. Using a conservative multiplier factor of five, the value to the Manitoba economy of the wolf pelts sold in 1980/81 was near a quarter of a million dollars.

On the debit side of wolf economics is loss of other furs to trappers by wolf depredation, loss to livestock owners of cattle killed or injured by wolves, and cost of wolf control programs. As there is no wolf control program for the benefit of wild prey and no compensation program for livestock loss caused by wolves, there is no provincial expenditure on these two categories.

As no central registry currently exists for recording various costs incurred as a result of wolf actions, data are superficial or lacking. This is partly because of the almost total elimination of wolf control programs in recent years. No direct costs for control were reported during 1980 and a cost of only $30 000 was recorded for 1979. No disbenefit costs are readily available for losses sustained by trappers or livestock owners. It is assumed that the total debits of the wolf economics are considerably lower than the total benefit to the provincial economy.

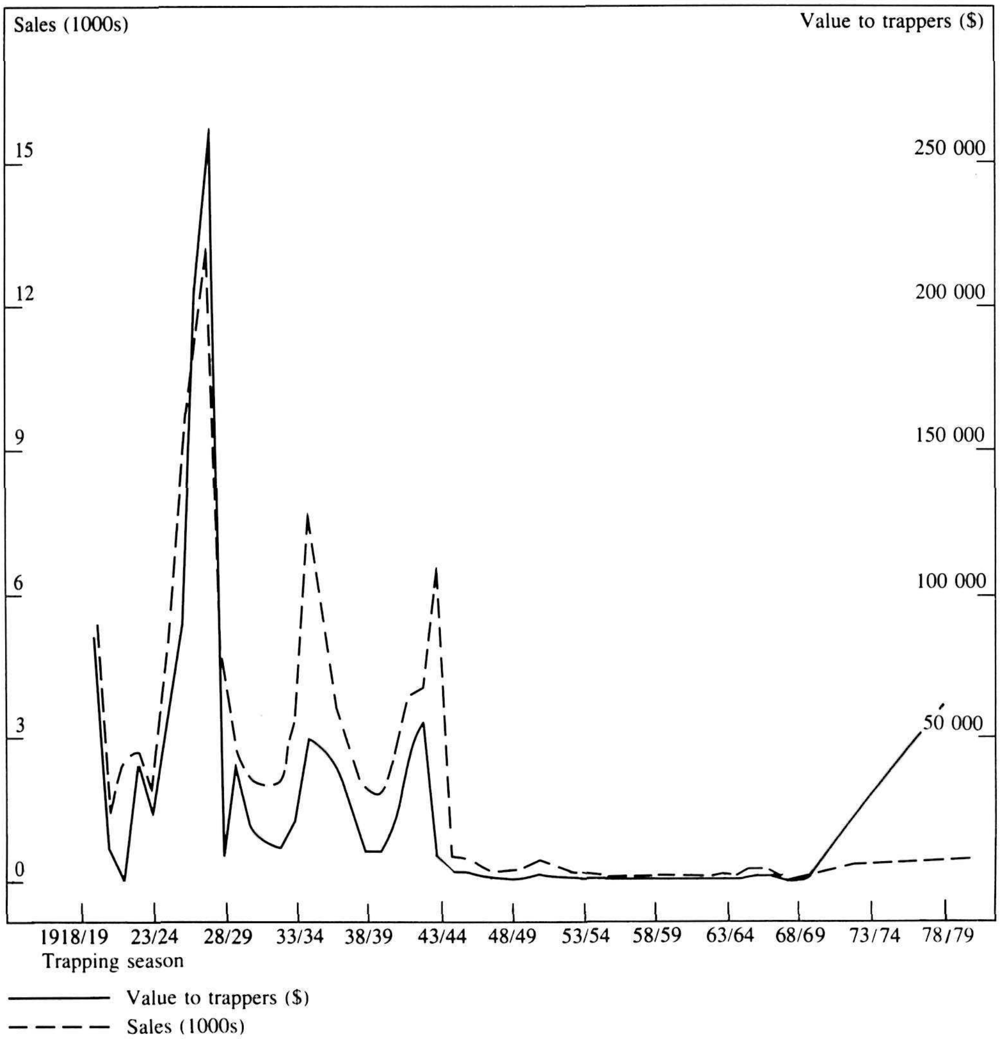
6. Management strategy

Following years of no designation under the Wildlife Act and a predator designation under the Predator Control Act, the wolf was classified as a big game species under a new Wildlife Act in 1980 (the Predator Control Act was repealed at the time). Wolves may now be hunted and trapped only under authority of a valid licence and during specified seasons. They may also be killed at any time in defence of property but there is no central recording mechanism to evaluate this kill.

Manitoba has recently begun development of management strategies for various wildlife species or groups of species. Wolves were

Figure 3
Wolf pelts marketed and value to trappers, 1918–81
(modified from Manitoba Fur Fact Book)

Figure 3



Trapping season	Sales	Value to trappers ($)	Average pelt price ($)
1966/67	213	3 408	16
1967/68	139	2 363	17
1968/69	118	3 186	27
1969/70	138	5 244	38
1970/71	167	3 841	23
1971/72	324	12 312	38
1972/73	332	17 596	53
1973/74	349	22 336	64
1974/75	395	24 490	62
1975/76	383	38 683	101
1976/77	464	36 192	78
1977/78	365	53 290	146
1978/79	358	59 070	165
1979/80	406	47 908	118
1980/81	422	39 246	93

identified as a species of sufficient importance to warrant a separate plan. General guidelines by which wolves will be managed over the next decade have been proposed.

The primary objective is to maintain the provincial wolf population at its current level of approximately 4000 animals. Major conflicts may arise in keeping wolf numbers stable while at the same time proposing to increase numbers of big game species such as moose (*Alces alces*), elk (*Cervus elaphus*), and deer (*Odocoileus* spp.). The guidelines envisage that the primary use of wolves should continue to be for hunting and trapping on a recreational and commercial basis with regulated licences and seasons. Implementation of a wolf inventory and research program is an essential component of the management strategy.

An equally important secondary objective is to convince the public that wolves are essential components of natural ecosystems. To achieve this aim there should be programs to provide the general public with information that will promote awareness and understanding of the species, and programs to encourage sound animal husbandry practices in fringe livestock production areas. Opportunities should be pro-

Visitors listening to a pack of wolves during a daytime interpretive field trip in Riding Mountain National Park, Manitoba (photo: K. Whaley)

vided for the public to listen to and view wolves in the wild.

Thirdly, wolves would be controlled on a site-specific reactive basis. Control would relate mainly to livestock depredations by wolves, and only the most humane, cost-effective, and practical methods would be used. Details of Departmental policy are currently being developed.

Status and management of wolves in Ontario

George B. Kolenosky

1. Abstract

Timber wolves remain as a controversial but important component of Ontario's fauna. They occur throughout most continuous forested areas and occupy about 85% of their historical range. In some areas, declines from peak levels in the mid-1960s have been associated with declines in major ungulate prey. Wolves are classified as furbearers and receive the same protection afforded other wildlife species in most sections of Provincial Parks and Crown Game Preserves. Limited control programs are conducted for protection of domestic livestock and in the vicinity of white-tailed deer wintering areas. Current management practices and recent changes in public attitudes will ensure the species' continued survival throughout most of its present provincial geographic range.

2. Introduction

The timber wolf (*Canis lupus*) remains one of the most controversial wildlife inhabitants of Ontario. Although attitudes towards predators are considerably more enlightened than they were 20–30 years ago (Theberge 1973), there is probably no single wildlife species in the Province that has generated more discussion among government personnel, hunters, trappers, naturalists, and other members of the public than the wolf. Research in North America and elsewhere during the past two decades has dispelled many earlier myths, such as the wolf's supposed danger to man and its bouts of excessive slaughter of prey, but debates about its relative value are still frequent and often highly emotional. Opponents view it as an undesirable competitor for desired big-game species such as white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*), whereas supporters regard it as an intelligent, highly social carnivore with an exemplary family life. Although personal opinions may differ, the importance of the species cannot be denied, or its presence ignored. This paper summarizes the classification, current status, distribution, relative density, and management of the wolf in Ontario.

3. Current status

3.1. Classification

Goldman (1944) recognized two subspecies in Ontario: *C. l. hudsonicus* adjacent to the Hudson Bay coast and *C. l. lycaon* throughout the remainder of the Province. On the basis of more recent studies (Kolenosky and Standfield 1975), we now recognize the following subspecies and types: *C. l. hudsonicus* in the Hudson Bay and James Bay coastal areas, *C. l. lycaon* (Boreal type) in the northern and central boreal forest, *C. l. lycaon* (Algonquin type) in the deciduous–coniferous forest, and a small wolf, *C. l. lycaon* (Tweed type) that occurs along the extreme southern edge of the range of the Algonquin type. Kolenosky and Standfield (1975) described morphological and food habit differences between the Boreal and Algonquin types.

The Tweed wolf has characteristics that suggest it may be a result of hybridization between wolves and coyotes (*C. latrans*). Hybrids similar in size and morphological appearance were produced in captivity by crossing a female Algonquin type wolf with a male coyote (Kolenosky 1971). Hybrids of that type remained fertile to at least the second generation (Kolenosky, unpubl.). If hybridization in the wild occurs, circumstances under which this happens vary, as in many cases wolf–coyote interactions result in the death of the coyote (Carbyn 1982*b*).

3.2. Distribution

Prior to colonization by European man in the 17th century, wolves probably occupied the entire Province (Bates 1958, Ont. Dep. Lands and Forests, unpubl. rep.). Early reports suggested they were common to abundant. However, initial references (Weaver 1913, Rich 1949) were too brief to permit any assessment of numbers or densities. As settlement increased, wolves were soon eliminated from southern Ontario (Standfield 1970).

Currently, wolves occur throughout the forested parts of the Province as far south as a line extending north of Lake Simcoe east to the northern part of Lanark county (Fig. 1). They have occasionally been recorded even farther south, but as these records were invariably of a single individual and not a resident population, those southerly sections are not considered to be normal wolf range (Kolenosky, Voigt, and Standfield 1978, Ont. Min. Nat. Resour., unpubl. rep.). Before 1950, wolves were sometimes found on the Bruce Peninsula (Peterson 1966), but there are no recent records of their presence. However, records of the Ontario Ministry of Natural Resources (unpubl.) show that a few do occur on Manitoulin Island. In general, the distribution of wolves closely approximates the southerly limit of exposed Precambrian rock, which supports a coniferous forest or a mixture of conifers and hardwoods. Approximately 85% of their historical range, which was the entire province, is still occupied by wolves. During the past 20 years, there has been little change in overall distribution.

3.3. Numbers

In the mid to late 1960s, estimates of total numbers ranged from 10 000 to 15 000 (Standfield 1970). Densities varied from 1/26 km^2 (Pimlott *et al.* 1969) in the more productive deer ranges of east-central and northwestern Ontario (Cumming and Walden 1970) to probably less than 1/500 km^2 along northern coastal areas. During the past decade, numbers have declined throughout much of the east-central and eastern parts of the Province as a consequence of declining deer populations. Areas with previous high wolf densities, such as Algonquin Park and surrounding regions, have probably experienced the greatest declines. Numbers are also believed to be lower in certain sections of the deer range in northwestern Ontario. More recently, declining moose populations throughout much of the southern boreal forest may have resulted in lower wolf populations, but there are no reliable data.

Estimates of current relative densities (Fig. 1) were derived from densities established during wolf studies in the 1960s (Pimlott *et al.* 1969, Kolenosky 1972), and updated in accordance with recent reports from regional and district field biologists. At present there are no specific wolf studies underway except in Algonquin Park, where an aerial survey of the original main wolf study area is carried out at least

Timber wolves in pursuit of a moose (photo: Rolf Peterson)

once each winter. In other sections of the Province, indices of abundance are derived from sightings of wolves and wolf tracks regularly recorded during aerial moose surveys and aerial surveys to delineate deer wintering areas.

Wolf densities are largely a function of ungulate availability (Pimlott 1967*b*), therefore future wolf density levels will be largely determined by the subsequent abundance of deer and moose in the province. During the start of deer declines in the early 1960s, wolves switched from deer to beaver (*Castor canadensis*) during the ice-free months (Hall 1971, Voigt *et al.* 1976) but ultimately their continued survival is dependent on adequate deer and moose populations (Mech 1970). Recent recovery of local deer populations in some sections of east-central Ontario will probably result in a higher wolf population (C.W. Douglas, pers. comm.).

4. Management

4.1. Current policies

In Ontario, wolves and coyotes are classified as furbearers (Ont. Reg. 242/80). Except for protection of personal property, a licence to hunt wolves is required by both residents and non-residents. In the northern part of the Province (north of the southern boundary of the regional municipality of Muskoka), licences are not available from 15 June to 1 September. South of this line, holders of resident small game licences may legally hunt wolves during that period by purchasing a special summer tag. Wolves are legal furbearers for holders of registered traplines; an export permit is required fo shipment out of the Province.

Importation of timber wolf pelts into th United States is prohibited by the US Endangered Species Act of 1973. The hunting of wolves in Ontario from aircraft or motorized vehicles is not permitted.

Figure 1
Wolf distribution and abundance in Ontario

Wolves are afforded the same protection in Provincial Parks and Crown Game Preserves as other species. However, some trapping is permitted in certain sections of some parks. In most cases, these are the areas where trapping was carried out before establishment of the park. The largest areas where wolves receive the most protection are Algonquin Provincial Park (7653 km^2), Chapleau Crown Game Preserve (7221 km^2), and Quetico Provincial Park (4744 km^2).

4.2. History of control

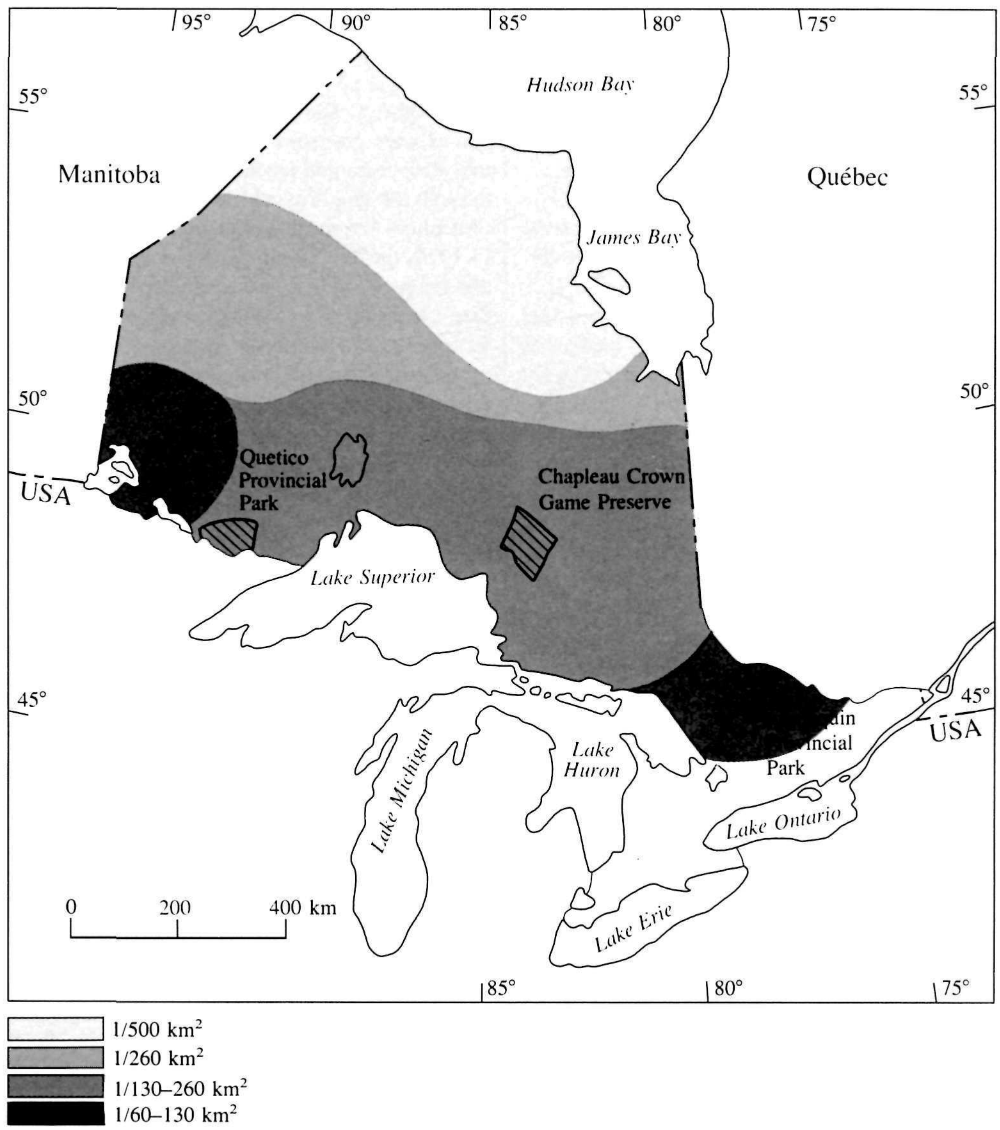
Traditionally, wolves were considered inimical to game and livestock species, and efforts to eliminate, or at least control them continued unabated for many years. A system of bounty payments was in operation in Ontario from 1793 until December 1972, although its value was frequently questioned (Cross 1937, Omand 1950). At the time it was rescinded, bounty payments were $25 per adult and $15 for a pup less than 3 months old. During the last 10 years of payments, approximately 1450 claims were made annually (Ont. Min. Nat. Resour., unpubl. records). Since 1925, over $2 000 000 has been spent on bounties for wolves and coyotes, but that expenditure has had little effect in controlling numbers of either species (Clarke 1970, Standfield 1970).

Both before and after removal of the provincial bounty, certain counties and townships, under authority of the Municipal Act, offered their own system of bounty payments, ranging from $5 to $85. These local bounties occurred only in the region east and south of Lake Huron where organized counties exist, but were made illegal in 1980 with the classification of wolves as furbearers. Although enforcement problems still remain in some local areas, the payment of bounties is gradually being phased out.

4.3. Control programs

In 1964, a Predator Control Unit was established by the then Department of Lands and Forests to provide control in specific areas and serve as an alternative to the bounty system. Currently, specific control of all predators is under the direction of this Unit within the

Figure 1



No valid hunting licences are available during the summer in the area south of the heavy black line adjoining Algonquin Provincial Park.

Ministry of Natural Resources. The Unit is not a separate entity, but consists of conservation officers, trained as predator control officers, who investigate complaints on demand. Approximately 100 officers have been trained since the inception of the program. However, only about 20 would be engaged in predator control activities during a particular year, and regular duties as conservation officers are still carried out.

All complaints of predation on domestic livestock or wildlife species are investigated by the local predator control officer. If control is deemed necessary, the officer has three possible courses of action. He may personally inaugurate a control program, may instruct the complainant in the proper use of traps or snares, or may engage a professional trapper. The third course is chosen most frequently in the vicinity of deer wintering yards where control is considered necessary to help maintain local deer populations.

In all control programs, emphasis is placed on the use of traps and snares, as they are considered to be the most selective and effective means of eliminating unwanted predators (Kolenosky, Voigt, and Standfield 1978, Ont. Min. Nat. Resour., unpubl. rep.). In the organized counties of southern Ontario, neck snares cannot be used without special permission. Poisons are not used, and in fact, those that are commonly promoted for predator control, namely strychnine, Compound 1080 (sodium fluoroacetate), and cyanide are prohibited by the Pesticides Act under the administration of the Ministry of Environment. In instances of predation on domestic livestock, participation by the complainant is actively encouraged because of his availability for checking sets and greater knowledge of the local area. To the greatest extent possible, control programs are directed toward removal of the offending individual or individuals.

The Ministry also provides training programs in the form of predator workshops. Interested persons are taught the proper use of traps and snares by a professional trapper or the local predator control officer. Approximately 2500 farmers and trappers have received instruction since the program was inaugurated.

4.4. Compensation for predator losses

A significant positive step in the management of wolves and coyotes was taken in 1972 with the elimination of the bounty and the passing of the Wolf Damage to Livestock Compensation Act. During the first 2 years, all claims were processed by the Ministry of Natural Resources and payments were made through the Dog Tax and Livestock and Poultry Protection Act and the regulations thereunder. In 1974, the Wolf Damage Act was repealed and the provisions in it were included in the Dog Licensing and Livestock and Poultry Protection Act and administered through the Ministry of Agriculture and Food. Authority to process claims remains under that Act to the present.

To receive compensation for losses due to predators, the owner must immediately notify a "valuer", appointed under the Act, of the death of or injury to the livestock and must retain the animal or its carcass until the investigation is completed. Action to protect the remaining livestock and indication of control measures that the owner will undertake must begin within 48 h of discovery of damage. If the claim is valid, the owner will receive payment up to the full market value of the livestock, to a maximum of $1000 for a head of cattle, $500 for a horse, $200 for a goat, $200 for a sheep, $200 for a head of swine, $100 for a furbearing animal, $1000 for poultry killed or injured in any year and $1000 for all rabbits killed or injured in any year. During the past 5 years, claimants for all predators have ranged from 282 to 417 annually and payments from $51 866 to $99 456 (Table 1).

Annual expenditure for predator control activities for the past 5 years was approximately $100 000. From 150 to 200 wolves and coyotes were taken annually as a result of these programs. About 90% of the control activities in agricultural areas deals with coyotes. Instances of wolf predation on livestock occur only sporadically because of low or nonexistent wolf populations in most agricultural regions. The farming areas of northwestern Ontario and the Claybelt section of northeastern Ontario are two regions with the highest frequencies of wolf–livestock interactions. During the past 3 years 20–40 wolves were removed annually for protection of livestock. However, it is difficult to provide a precise breakdown of species because of difficulties in identifying canids in certain sections of the Province (Kolenosky 1971).

A policy that authorizes predator control for the benefit of recreational species (ungulates) was introduced in 1980. Previously, control was officially limited to agricultural problem areas. Included in this policy is authority to use aircraft for control purposes if considered necessary. To date, aircraft have not been used, and their future use is expected to be minimal.

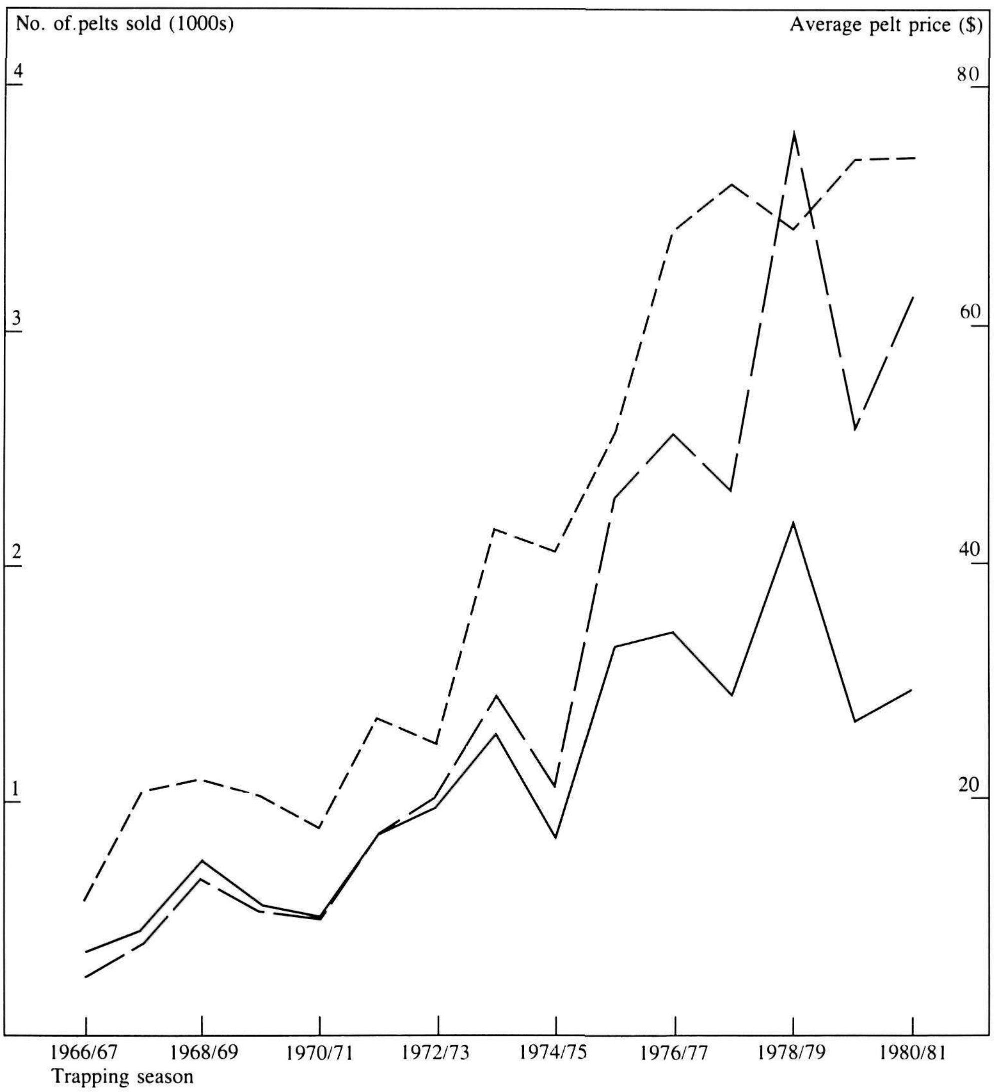
At present the control of wolves to protect other wildlife species is practised only in the vicinity of deer wintering areas. Most control activities are confined to specific yards where programs of deer range improvement are conducted (Douglas 1964). Most of these are located along the northern edge of deer range in the east-central and eastern portions of the Province (Smith and Borczon 1977). The need for

Table 1
Claims and payment under the Dog Licensing and Livestock and Poultry Protection Act, Ontario

Year	No. of claimants	No. of claims	Payments ($)
1973	313	1005	51 866.00
1974	390	1281	71 699.11
1975	345	1951	80 833.85
1976	282	1640	70 308.30
1977	417	1535	98 891.54
1978	404	1984	99 455.66

Figure 2
Fur harvest returns from Ontario

Figure 2



———— Adjusted average pelt price
—— —— Average pelt price
— — — — Sales
(Consumer dollar = 1.0 in 1971)

Trapping season	Sales	Average pelt price ($)	Adjusted average pelt price ($)
1966/67	576	5.91	7.09
1967/68	1046	7.88	9.14
1968/69	1093	13.44	14.92
1969/70	1027	10.63	11.27
1970/71	883	9.84	10.14
1971/72	1353	17.08	17.08
1972/73	1236	20.56	19.53
1973/74	2140	28.84	25.67
1974/75	2060	20.82	16.66
1975/76	2561	45.57	32.81
1976/77	3397	50.94	34.13
1977/78	3601	46.09	28.58
1978/79	3352	76.02	43.33
1979/80	3434	50.98	26.51
1980/81	3394	62.15	29.21

control around specific yards is assessed annually and on an individual basis by local managers.

In the extensive Loring deer yard complex southwest of North Bay, where numbers of wintering deer may approach 10 000 (Wolfe 1979, Ont. Min. Nat. Resour., unpubl. rep.), limited control of wolves has been part of the deer rehabilitation program for the past 10 years. During the past 5 years, approximately 20 wolves have been removed annually; trapping and snaring were the only methods used. Total removal throughout the Province for the benefit of other wildlife species would be less than 40 per year.

The use of dogs to hunt coyotes and wolves is becoming an increasingly more important recreational pursuit in sections of southern Ontario. Much of this activity occurs in semi-agricultural areas where coyotes are the main quarry but a few wolves are taken annually. Dogs have not been used with any success in the more rugged, continuous wolf range of the Precambrian Shield.

4.5. Pelt sales

The recent popularity of long-haired furs has resulted in a significant increase in the sale of coyote and wolf pelts during the past 14 years (Fig. 2). Within the past decade sales have tripled and average prices have increased almost four times in real dollars. During the past few years, annual sales have exceeded $250 000. Unfortunately, sale records do not accurately differentiate between timber wolves and coyotes, so the actual number of each species remains unknown. Failure to designate species circumvents the prohibition on importation of wolves into the US under the Endangered Species Act of 1973; sales are legalized by simply classifying all wolf or coyote pelts as coyotes.

4.6. Future status

The future of the wolf in Ontario appears reasonably secure at present. Although wolves were eliminated from most of the agricultural areas 100 years ago, they are probably as numerous today as they were in more primitive times. Numbers, however, have declined in many sections of the Province from peak levels in the mid to late 1960s. Future population levels will be largely dependent on future densities of deer, moose, woodland caribou (*Rangifer tarandus caribou*), and to a lesser extent, beaver.

Current management policies will ensure the survival of the wolf in most forested areas, but destruction of habitat, which is probably the main factor limiting wolf numbers (Kolenosky and Standfield 1975), could result in the elimination of some local populations in the future. However, recent changes in public awareness and concern make me optimistic that the wolf will remain as an important member of Ontario's fauna.

4.7. Requirements of a national conservation strategy

I feel the development of any national conservation strategy for wolves should include the following components:

1. Classification as a game animal or furbearer. The importance of the species must be recognized to ensure necessary concern and the enactment of adequate protective legislation.
2. Allowance for specific control, where and when needed. Any management scheme should be flexible and acknowledge that undesirable predation on domestic livestock, and occasionally on wildlife species, will occur. Selective and limited control of wolves will therefore be required in certain circumstances.
3. Inclusion of some form of compensation payments. It is unrealistic to expect farmers and ranchers to absorb all losses caused by wild predators.
4. A continuing public education program explaining the role of the wolf in natural and disturbed ecosystems. One of our best allies is a well-informed public. Support of any strategy requires understanding.
5. Investigation of the taxonomy of local races and types. Maintenance of extant or genetic strains requires knowledge of their existence and ecological requirements.
6. Continuation of research to enhance our understanding of the wolf's role in various ecosystems and how the species reacts and adjusts to increasing human intrusion.

5. Acknowledgements

I wish to thank the provincial regional biologists for providing contemporary information about population levels and control programs. A special acknowledgement is extended to D.R. Voigt and M. Novak for review of an early draft. N. Carter drafted the map and J. Robinson did the photography.

Status and management of wolves in Québec

A pair of wolves travelling along a frozen water course (photo: Rolf Peterson)

Daniel Banville

1. Abstract

This paper describes the status of the wolf in Québec in 1981. At the beginning of colonization, the wolf was found throughout the Province; it is now absent from the southern part of the Province so that its present distribution covers about 90% of its original range. Despite the scarcity of available data on absolute wolf densities for Québec, it is considered that the wolf is still thriving; its abundance is estimated at 1 wolf/100–1000 km^2 north of the 52^o parallel and 1 wolf/50–100 km^2 farther south. The wolf can be hunted throughout the year in Québec, except in provincial parks and reserves where it may only be hunted during the moose hunting season; trapping is allowed in season. In the southwest part of its distribution, the wolf is controlled in some white-tailed deer winter yards; in 1979–80 a maximum of 34 wolves were killed. Economically, the wolf is important as a furbearer; the annual harvest ranges from 400 to 600 wolves, yielding between $80 and $100 a pelt. Wolf hunting is marginal and wolf kills are mostly haphazard and fortuitous. In Québec, the wolf is not endangered and studies underway should afford more insight into its role as a predator of big game species.

2. Introduction

The wolf (*Canis lupus*) has undoubtedly evoked more controversy than any other species of wild animal in North America since its first contact with man at the beginning of colonization. Even today, although we have a better understanding and acceptance of its ecological value, the mention of its name still evokes an image of 'the big bad wolf'.

The province of Québec has used methods similar to those of most American states to control the wolf when predation on domestic animals becomes a problem. From the middle of the 19th century until today the wolf has been persecuted almost without respite, either because it was responsible for the loss of a few sheep or calves (up to 1960) or because the losses it inflicted on our declining deer population (*Odocoileus virginianus*) were considered intolerable (since 1965). Various control methods were instituted to eliminate the problem, beginning with the payment of a bounty (abolished in 1971), then by the hiring of special control personnel (1960–70), and finally through a control program based on predator-management principles and a better understanding of its value and place in nature (Berryman 1972, McCabe and Kozicky 1972). For more details and information on the history and the results of the control of predators in Québec, see Banville 1981.

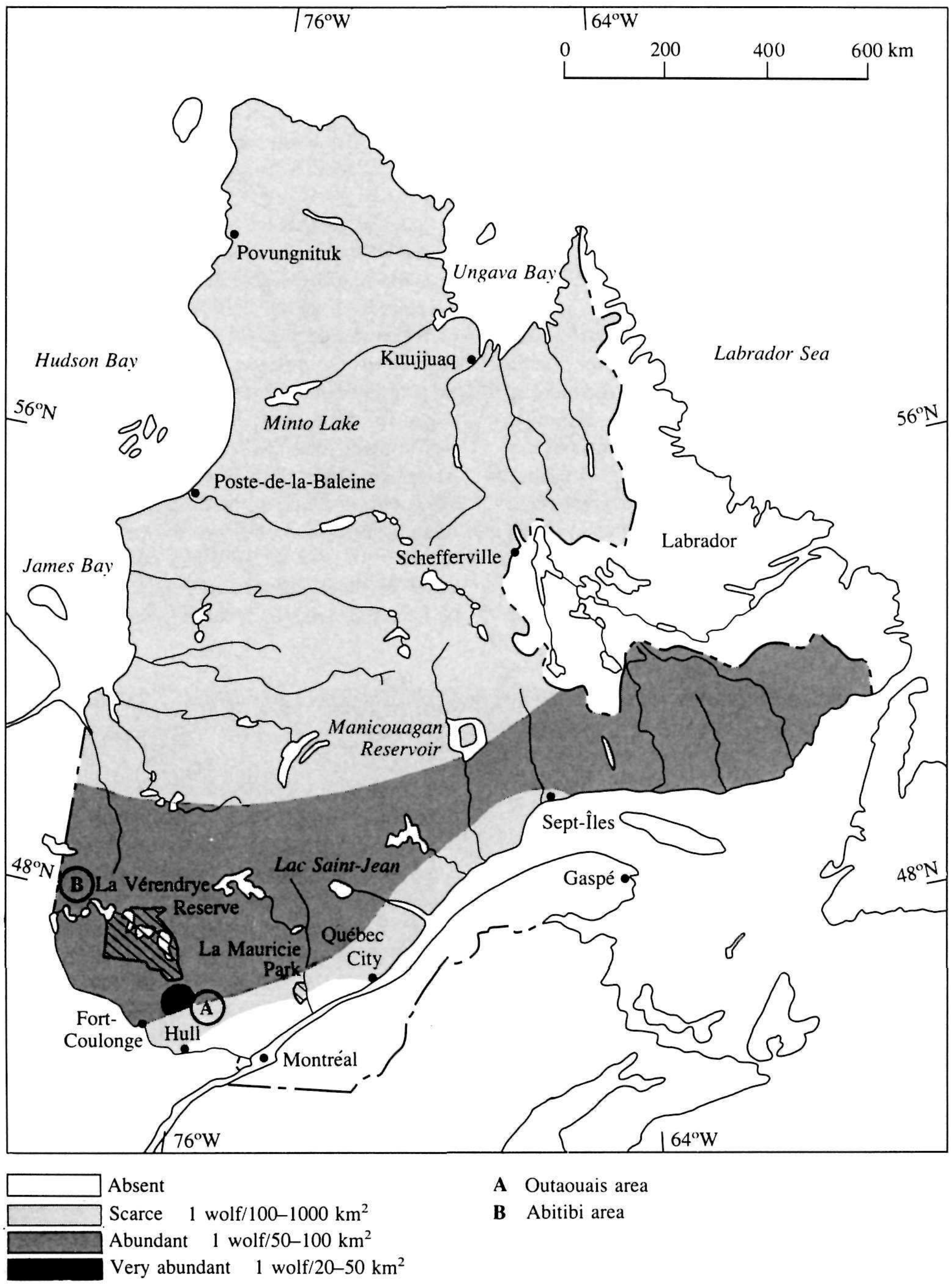
3. Distribution and abundance

As a result of persecution and progressive elimination of suitable habitat by forest exploitation and urban and agricultural development, the wolf is now confined to the more remote sectors of the Province. At the beginning of colonization, wolves ranged throughout the Province, but are now no longer found south of the St. Lawrence River; they were probably exterminated from this region by the end of the last century (Young 1944) and have since been replaced by the coyote (*Canis latrans*), which immigrated into Québec around 1944 from the northern American states and southeastern Ontario (Georges 1976, Lord 1961). North of the St. Lawrence, wolves are no longer found where forest has given way to farming and urbanization; this encompasses an area that progressively increases in width from Québec city to Ottawa and is about 80–100 km wide at Montréal. However, the wolf is still found in Québec in about 90% of its original range (Fig. 1).

No systematic study, on either a provincial or a regional scale, has ever been undertaken in the province of Québec to determine the abundance of the wolf. The acquisition of such knowledge requires an immense investment in time and money, which although justifiable, has never been made. However, rough estimates of the density of wolves in the province can be made from studies of wolf predation on white-tailed deer (Banville 1979, Stephenson 1973, unpubl.) and on preliminary results of a study on predation of moose (*Alces alces*) being carried out in the southern part of La Vérendrye Reserve, which has an established wolf density of 1 wolf/70 km^2 (F. Messier, pers. comm.).

Figure 1
Relative distribution and abundance of the wolf in Québec

Figure 1



I have divided densities into four categories (Fig. 1): (1) absent; (2) scarce — presence of solitary wolves or small, widely dispersed packs, corresponding to 1 wolf/100–1000 km^2; (3) abundant — presence of uniformly dispersed wolf packs corresponding to 1 wolf/50–100 km^2; (4) very abundant — wolf pack concentration corresponding to 1 wolf/20–50 km^2.

4. Legal status

In Québec the wolf is classified as a furbearing animal. Trapping of wolves is governed by provincial regulations which stipulate that wolves may be trapped, depending on the zone and with the appropriate permit, between 11 October and 15 April. Regulations in force for 1980–81 do not place a limit on the numbers of wolves taken. Before 1980 the wolf could have been trapped throughout the year.

For sport hunting, the species may be hunted either for itself or concurrently with small or big game, for which the respective permits allow hunting of wolves without a bag limit. There is, however, no specific permit for the wolf and no closed season, as is also the case for coyotes, woodchucks (*Marmota monax* and porcupine (*Erethizon dorsatum*), which are considered undesirable species.

In the seven parks or wildlife reserves within the distribution limits of the wolf where a controlled moose hunt is allowed, a single wolf may be taken per moose permit. The wolf is therefore not completely protected in provincial parks or reserves; it is only protected because big game hunting is not allowed during most of the year. In fact, the only place where the wolf is truly protected from all forms of exploitation is in La Mauricie federal park, which covers an area of 542 km^2.

5. Wolf control

Wolf control in Québec has been established because of predation on domestic animals. At the moment, however, control of this predator is only undertaken to afford protection to white-tailed deer in their winter yarding areas.

Predation on livestock is often caused by coyotes that have invaded the ecological niche left vacant by the retreat of the wolf to remoter areas. A few isolated cases may be attributed to the wolf but no compensation is given for these losses; wolf predation on farm animals is considered a marginal problem in Québec. In farming areas, attention is chiefly directed to losses caused by coyote predation. Areas with wolf–livestock problems are marked as A (Outaouais) and B (Abitibi) on Figure 1. Of all the complaints received, less than 20% can be attributed to wolves. North of Montréal, where such problems used to be reported in the past, no similar records of wolf predation have been recorded within the last 3 years.

In the early sixties, hunting of white-tailed deer reached an unprecedented peak; as a result the deer population began to decline. During this period, predation by wolves in the wintering yards, which was reported to the public in a biased manner by some sports writers, was interpreted by many as being the sole cause of the deer decline. During the winter of 1965–66, a governmental wolf control program was established for the first time. A special control team composed of 6–10 men was assigned to control wolf populations, using all the means available at that time — traps, snares, firearms, poison, etc. In 1967, this activity was under the sole responsibility of the Conservation Service.

In 1971, because of administration problems relating to this policy, a new and better-organized program was instituted. The fundamental idea of this program was to control wolf populations in and around deer wintering yards, where the effects of wolf predation were deemed undesirable. This program is still in effect today (Banville 1981).

At present, control of wolves is restricted to deer wintering yards found at the northeast limit of deer range, which corresponds to the area encompassed by Montréal, Fort-Coulonge, and the southern part of La Vérendrye Reserve. Since 1971 the annual harvest has varied between 22 and 55 animals; in 1979–80 34 wolves, at most, were killed.

No control of wolf populations is undertaken at the moment to protect moose, mainly because predation on this species is less evident and because we have no precise idea of its extent and impact. We do suspect, however, that predation mortality (especially on calves in summer) may be important and may have a negative effect on moose population growth in certain areas of Québec (Crête *et al.* 1981). A study, of which one of the principal aims is to determine the importance of wolf predation on moose, is currently being conducted in the southern part of La Vérendrye Reserve. The results of this study should throw some light on the moose–wolf relationship in Québec.

6. Economic importance

The economic importance of the wolf is almost exclusively related to its status as a furbearing animal. Predation by wolves on farm animals is negligible, and no form of compensation has been awarded since 1971, when the bounty system was abolished. We are beginning to realize that the wolf played an important role in the decline of deer during the period 1965–75 (Huot 1977, Transact. 11th meeting of the N.E. deer group), as has been observed elsewhere, especially in Minnesota (Mech and Karns 1977). The wolf has also been the direct cause of the disappearance of certain deer yards at the northernmost limit of deer distribution (Banville 1979). However, it is very difficult to quantify (in dollars) what part of the deer decline could be directly attributed to the wolf.

As a furbearing animal, the wolf is not a species sought after by Québec trappers, who prefer to trap more abundant species. Those who do trap for the wolf frequently do so concurrently for other species, setting out a few traps without any real conviction and counting themselves lucky if they get a wolf.

Until 1977–78 the pelts of wolves and coyotes were classified together in the official records of pelt harvests, so it is impossible to obtain exact figures for the number of wolves trapped in Québec in past years. However, for the years 1978–79 and 1979–80, when coyote and wolf pelts were recorded separately, the harvest of wolves was 553 and 532 respectively. These results suggest that between 400 and 600 wolves were harvested annually since 1972 (Leblanc, pers. comm.). Most of these wolf pelts were obtained from registered traplines and beaver reserves. The average value of a pelt was approximately $20 in 1972–73. This market price increased progressively to about $80 by 1978–79, and has remained at this level ever since. According to the number of pelts sold and the total price obtained, the wolf places 14th among the 15 most common furbearing animals in Québec.

Finally, although wolf hunting is allowed throughout the year almost everywhere in Québec, it attracts few people. The few wolves that are taken by hunters (no available statistics) are for the most part the result of a fortuitous meeting while hunting big game.

Conclusion

In spite of unrelenting persecution of wolves and their disappearance south of the St. Lawrence River, the species is still considered to be thriving in Québec. It is in no danger of extinction. Until now the two principal types of human exploitation of the wolf, governmental control and trapping, have had little effect on its abundance and distribution, except locally. Moreover, as far as the governmental control program is concerned, no fundamental new changes are foreseen in the near future; trapping still remains the principal form of exploitation and we believe that the harvest will remain stable in years to come.

In Québec it seems that the time when the wolf was hated without really knowing why is gone. The wolf is increasingly being considered as an interesting element of our wildlife heritage. It is evident that we must achieve a better understanding of the role that predators of big game play if we are to improve our wildlife management methods, in which the principles of conservation and rational exploitation should be fully integrated.

Historical and present status of wolves in the Northwest Territories

Douglas C. Heard

Abstract

Relatively few wolves were killed in the NWT before 1924, when a $30 bounty payment was first introduced. During the 13 years of bounty payments, from 1924 to 1933 and from 1937 to 1939, an average of 1000 wolves were killed annually. Concern about a decline in barren-ground caribou populations led to a major wolf poisoning program on caribou ranges east of Great Bear Lake from 1951 to 1964. Wolf numbers appeared to have been reduced but they probably recovered quickly. Extinction of wolves on Southampton Island in the early 1950s occurred because caribou were exterminated by overhunting. Caribou were reintroduced to the island in 1967 and wolves have returned through natural immigration. Wolf numbers were reduced by trapping and aerial shooting in the Slave River lowlands as part of a program to halt the decline of the bison herd. The wolf control program was discontinued when hunters failed to reduce their killing of bison voluntarily. At present, wolves occupy all of their traditional range in the NWT and natural densities prevail in most areas. Density is highest on barren-ground caribou winter range and lowest on Victoria Island and the Queen Elizabeth Islands. The annual kill of wolves has increased during the last 20 years, probably because of rising pelt prices and the availability of snowmobiles for hunting wolves.

1. Historical status

1.1. Before 1950

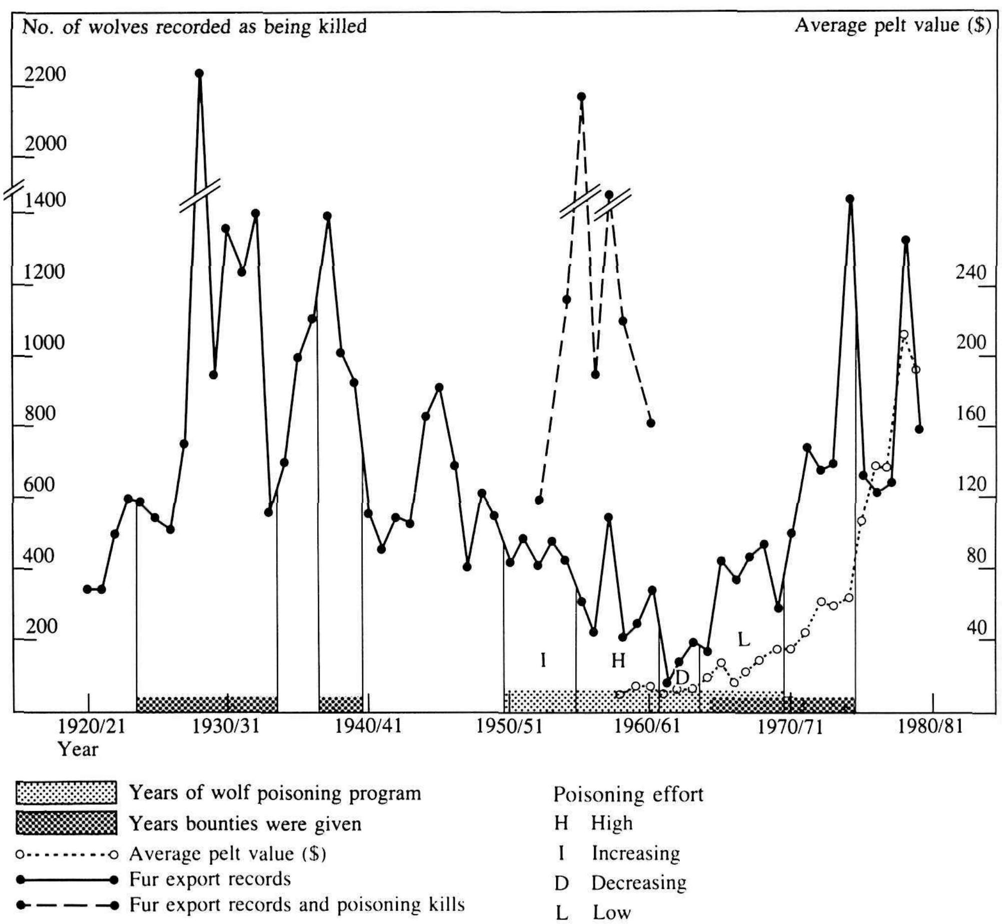
Relatively few wolves (*Canis lupus*) were killed in the NWT before 1924 (Freeman 1976), when the first wolf bounties were introduced. Wolf hides had little commercial value and the religious beliefs of some Indians inhibited killing of wolves. The $30 bounty payment introduced in 1924 when white fox (*Alopex lagopus*) pelts, the mainstay of the high Arctic fur trade, were selling for only $15 was a considerable incentive to hunters and trappers and the wolf kill increased (Soper 1928). In addition, the number of trappers (mainly from Scandinavia and southern Canada) substantially increased during the early 1920s in response to high fur prices (Usher 1971). About 1000 wolves were killed during each of the 13 years when bounties were paid (1924–33 and 1937–39, Fig. 1). After bounty payments were discontinued, the average annual wolf kill dropped to less than 700 (1934–36 and 1940–49). The change in the number of wolves killed was also related to the change in the number of trappers on the land. From 1938, trapping was restricted to Indians, Inuit, and non-natives who already held a permit (Usher 1971); in addition, the number of trappers declined during the 1940s because men left to fight in World War II.

1.2. 1950 to present

The number of wolves killed increased sharply in the mid-1950s (Fig. 1). In 1948, the first range-wide aerial surveys of caribou (*Rangifer tarandus groenlandicus*) indicated that mainland barren-ground caribou populations were considerably smaller than expected and were believed to be declining rapidly (Banfield 1954, Kelsall 1968). Because wolves were known to be the major predator on barren-ground caribou (Kuyt 1972), biologists believed that a reduction in the wolf population would buffer what was considered to be the real cause of the decline — overhunting. The wolf control

Figure 1
Number of wolf pelts exported from the Northwest Territories each year since 1920

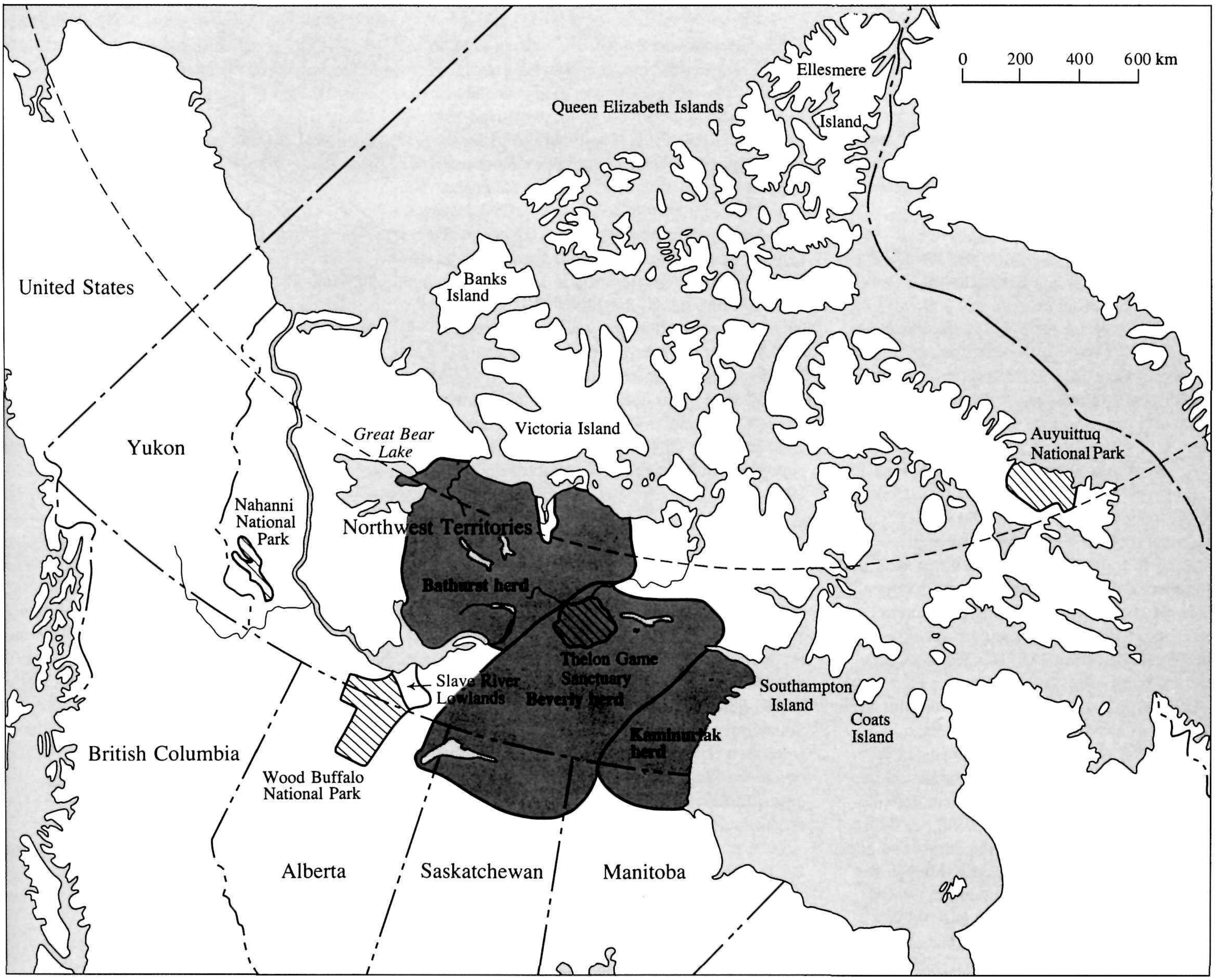
Figure 1



Source: NWT Wildl. Serv. files.

Figure 2
Map of the Northwest Territories showing major caribou herds where wolf populations were studied

Figure 2



program begun in 1951 involved strychnine-laced baits being placed on caribou winter ranges by government biologists and predator control officers. The poisoning program expanded each year until, by the winter of 1955/56, baits were being distributed on nearly all caribou-occupied winter ranges between Great Bear Lake and Hudson Bay (Fig. 2). Control efforts remained high until 1960/61 when it was concluded that "control" had been achieved (Kelsall 1968).

Each year between 1955/56 and 1960/61, the poisoning program in the NWT and in northern Manitoba and Saskatchewan accounted for the deaths of an average of 1800 wolves, but the average for the NWT alone was only 975 (Kelsall 1968). In addition, an average of 306 hides were exported annually from the NWT, bringing the yearly recorded kill to about 1300 (Fig. 1). Some of the wolves exported were probably taken as part of the wolf control program (and were thus counted twice) but fur export records underestimate the actual kill by the number of hides used within the NWT. The magnitude of these biases is unknown.

Kelsall (1968) concluded that wolf populations on the caribou ranges were substantially reduced by the wolf poisoning program because between 1955 and 1960 the number of wolves killed declined from 1755 to 450, the kill decreased from 44 wolves/$1000 expended to 14 wolves/$1000, and the proportion of pups in the population increased from 13 to 73%.

The poisoning program reduced the number of adult wolves in the population but the number of pups apparently increased. Between 1955 and 1960 the adult kill per dollar spent declined by 90% and the number of pups killed per dollar spent doubled. Although the wolf control program did not end in 1960/61, effort was reduced each year until 1963/64 when poisoning was finally eliminated from most areas; however, one predator control officer continued to poison wolves in northern Saskatchewan and the adjacent NWT until 1970. In 1965/66, against the advice of Canadian Wildlife Service biologists, a $40 wolf bounty was introduced throughout the NWT to give some economic assistance to trappers. Bounties continued to be paid until March 1975, although the legislation providing for those payments was not revoked until June 1980.

1.2.1. Banks Island

During the massive poisoning program of the 1950s, strychnine was easily available and was used extensively on Banks Island between 1955 and 1959. The justification for poisoning was to reduce wolf depredation on trapped foxes (Usher 1971), but a convenient side effect was that poisoning also killed foxes, providing extra pelts for trappers. Usher (1971) believed that poisoning reduced wolf numbers on Banks Island and resulted in low wolf densities there throughout the 1960s. Poisoning may have reduced the number of wolves but it was probably intense hunting that kept numbers low. Hunting still appears to be keeping wolf numbers relatively low (less than 1 wolf/260 km^2) (Beak Consultants Ltd. 1975, Banks Island Studies; Panarctic Oils Ltd.) considering the large population of potential prey (Vincent and Gunn 1981).

1.2.2. Southampton Island

Wolves were extinct on Southampton Island (Fig. 2) by the time the last caribou (their major prey) was shot in 1955 (Parker 1975). Forty-eight caribou were introduced to the Island in 1967 and as of 1980 the population has grown to over 1000 animals (NWT Wildl. Serv. files). One wolf was shot on Southampton Island in 1980 and tracks of others were seen. Undoubtedly those wolves crossed on the ice from the adjacent mainland and I suspect a resident population will soon become reestablished on the island.

1.2.3. Slave River lowlands

The most recent wolf control program in the NWT occurred in the Slave River lowlands (Fig. 2) in 1978 and 1979 as part of a program designed to reduce the rate of a decline in the bison (*Bison bison*) population.

Between 1959 and 1974 the Slave River lowlands bison herd fluctuated between 1500 and 2100 animals (G. Calef, no date, Status of bison in the NWT, NWT Fish and Wildl. Serv., unpubl. progr. rep.). In 1968 and 1970 a bison sport hunting season was opened for non-native

Figure 3

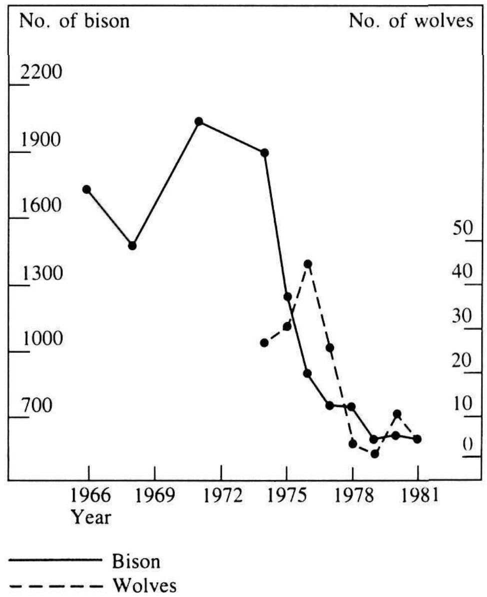


Figure 3
Number of wolves and bison observed in the Slave River lowlands, 1966–81

NWT residents and non-residents respectively. Between 1970 and 1974 native and sport hunters killed an average of 150 bison annually.

During the winter of 1974/75, ice and crusted snow reduced food available to bison in the Slave River lowlands. Many bison starved while others, in their weakened condition, became more vulnerable to wolf predation (J. Van Camp, pers. comm.). The bison population declined from an estimated 1900 animals to 1250 between March 1974 and March 1975 (Fig. 3). By March 1976 the wolf population had increased (as indexed by the number of wolves seen during the annual bison counts), perhaps as a result of the increased number of carcasses and weakened individuals; and the bison population declined to 900 animals.

Both wolf and bison populations declined between March 1976 and March 1977, when 26 wolves and 750 bison were counted. Van Camp (pers. comm.) suggested that a theoretical model proposed by Haber *et al.* (1976) for a wolf–moose system could explain his observations. The model predicts that in a stable predator–prey system, subject to even moderate hunting pressure (3–5%), a natural perturbation such as the severe winter of 1974/75 is likely to trigger a drastic prey decline, with both predator and prey population sizes stabilizing at a much lower density. The solution to such a situation requires the reduction of *both* hunting and natural predation until the prey population increases above some undetermined level. The NWT Wildlife Service has attempted to manage bison on the basis of this model.

In November 1977 wolf control was begun, with the aim but not the expectation of exterminating wolves from the bison herd's range. This control was generally supported by the local residents. Professional trappers who normally worked in the area were offered an incentive of $300 for each wolf. Trappers retained the hide, worth about $180. Bison sport hunting seasons were closed and native hunters were asked to shoot fewer animals, although their hunting remained unregulated. Thirty-four payments were made to trappers by March 1978 when the NWT Wildlife Service tried to eliminate the remaining wolves by aerial shooting. Ten were shot from a helicopter. Unfortunately, hunters did not restrict their shooting of bison and killed about 50 animals that year. Nevertheless, the bison population did not decline between March 1977 and March 1978 (Fig. 3) and only four wolves were seen during the March 1978 survey. The herd experienced a further setback when at least 39 bison died of anthrax during the summer of 1978. During the following winter, trapping incentive payments were made for 28 wolves. There was no spring aerial hunt. Again hunters did not substantially reduce their bison kill. Only two wolves and 600 bison were counted in March 1979 (Fig. 3). Because of the lack of hunter co-operation, wolf control was stopped and both predator and prey numbers appear to have stabilized at a lower level.

1.3. Present status

Although wolf densities have been reduced in some areas of the NWT through man's influence on the ecosystem, e.g. Southampton Island and the Slave River lowlands, wolves now occupy all of their traditional range. The only place in the NWT where there is a naturally occurring prey population but no wolves is Coats Island in Hudson Bay (Fig. 2). Wolves are not able to colonize the island because it is surrounded by open water even in winter.

Estimates of wolf densities in the NWT are rare. In general, the lowest wolf densities are found on Victoria Island and the Queen Elizabeth Islands (Fig. 2) and the highest are found in association with wintering concentrations of barren-ground caribou. On southern Ellesmere Island, Riewe (1975) estimated that in the area of greatest wolf concentration, density was only 1 wolf/900 km^2. In April 1979 I estimated at least 250 wolves associated with a large segment of the Bathurst caribou herd (Fig. 2) in an area of 1600 km^2 (1 wolf/6.4 km^2, NWT Wildl. Serv. files). Parker (1973) found 1 wolf/20 km^2 in February 1968 on the winter range of the Kaminuriak caribou herd (Fig. 2) in northeastern Saskatchewan and northwestern Manitoba. Kelsall (1968) estimated that there may be 8000 wolves on all barren-ground caribou ranges combined (1 wolf/160 km^2) while Parker (1972) estimated wolf density on the Kaminuriak herd's range at about 1/500 km^2.

In the NWT Wildlife Ordinance, wolves are classified as both big game animals and fur bearers. For most hunters and most areas there is neither a season nor a bag limit. Only in the Thelon Game Sanctuary (Fig. 2) are wolves completely protected. Hunting by Indians and Inuit is permitted in all three national parks; Wood Buffalo, Nahanni, and Auyuittuq (Fig. 2). Most wolves are shot after pursuit by snowmobile but a few are trapped. The number of wolves killed has increased markedly since 1961/62 (Fig. 2), probably because of the rising pelt value (Fig. 1) and the increased use of snowmobiles. The value of wolf hides exported from the NWT reached a peak of $280 000 in 1978/79.

1.4. Future status

The present policy of the NWT Wildlife Service is that wolf control will not be undertaken unless there is evidence that an ungulate population is declining at least partly as a result of wolf predation. Three of the four major barren-ground caribou populations, the Kaminuriak, Beverly, and Bathurst herds (Fig. 2), appear to be declining because of the combined effects of hunting and wolf predation (Simmons *et al.* 1979; Thompson and Fischer 1979; Heard 1980, unpubl. rep.). Temporary reduction in wolf numbers on these caribou ranges is being considered by the NWT Wildlife Service as part of a management plan designed to increase the herd size. Unless the Kaminuriak, Beverly, and Bathurst herds are preserved, wolves will probably disappear from large areas as they have from Southampton Island. Temporary reduction in wolf numbers, as long as it is accompanied by hunting restrictions, should be beneficial to the long-term survival of both caribou and wolf populations.

2. Acknowledgements

I appreciate the help received from Susan Fleck, Bruce Stephenson, Rupert Tinling, and Douglas Urquhart during the preparation of this paper.

The status and management of the wolf in the Yukon Territory

Bernard L. Smith

1. Abstract

Wolves range over the entire territory; however, little is known of their subspecies distribution, population status, and influence on prey populations. Management since 1919 is reviewed. Current wolf harvest regulations offer liberal yet traditional hunting and trapping opportunities. Wolf depredation on livestock is infrequent because livestock numbers are low. There is no compensation to livestock owners for losses. By necessity, wolf management currently receives limited attention.

2. Introduction

Wolves range over the entire Yukon from lowland forests to alpine and arctic tundra regions. Nowak's (1979) review of wolf distribution suggests the following subspecies, identified between 1905 and 1943, could still occur in the territory:

1. *Canis lupus ligoni* (Alexander Archipelago wolf), Goldman 1937
2. *C. l. mackenzii* (Mackenzie Tundra wolf), Anderson 1943
3. *C. l. columbianus* (British Columbia wolf), Goldman 1941
4. *C. l. occidentalis* (Mackenzie Valley wolf), Richardson 1829
5. *C. l. pambasileus* (Interior Alaskan wolf), Elliot 1905
6. *C. l. tundrarum* (Alaska Tundra wolf), Miller 1912

These subspecific distinctions were based on skull measurements from a limited number of samples; fewer subspecies may actually be present. Morphological measurements of a larger sample from interior and arctic Alaskan wolves have shown clinal patterns in skull measurements (Pedersen/1982) instead of the discontinuous patterns suggested by the earlier smaller samples.

Departures from naturally regulated wolf populations in the Yukon probably began in the 1740s with fur trading by natives with Russians in what is now southeastern Alaska. This trade was taken over by traders from the Hudson's Bay Company in the late 1840s and remained stable until the influx of miners during the 1896–99 goldrush. Many of the gold seekers turned to trapping and by 1910 much of the Yukon was depleted of some fur species. Harvest records were sketchy until the government instituted a tax on the export of raw furs in 1919 (data from before this date have not been compiled). In the 1920s the mean annual pelt export amounted to 163 wolves. After 1921, non-native trappers used strychnine (under government permit) to increase their efficiency, and between 1923 and 1929 trappers with the highest wolf harvest were paid \$500, \$300, and \$200 incentives. In 1929, a \$30 per wolf bounty was paid and 43 wolves were taken. In the early 1930s fur exports were low (mean 25 per year) until the bounty was repealed in 1933. Annual bounties were paid during this period on an average of 372 wolves. The use of poison was prohibited in 1931, but this restriction could not be enforced; as a result, during the rest of the 1930s the highest known wolf fur exports were achieved, averaging 473 wolves. In the first half of the 1940s an average of 261 wolves were exported annually. A \$20 bounty was in effect from 1946 to 1953 but no data are available on the numbers of claims submitted. During this period, wolf pelt exports dropped to 42 annually and remained low in the 1950s (mean 31 per year). Government predator control experiments began in the 1950s with cyanide guns. This was followed by increasingly extensive programs using aircraft placement of up to 154 poison baits throughout the territory. Baits were located in areas where wolves were believed to be numerous, on the basis of reports by trappers, the RCMP, and big game outfitters. Generally these programs were poorly monitored. After three winters of poison baiting, W.A. Fuller, Yukon's first biologist, attempted to monitor the program. Comparing the relative success of NWT and Yukon poisoning programs (as measured by wolf carcasses found in the late spring per bait) in the winters of 1956/57 and 1957/58, he suggested that wolves at that time were much less abundant in the Yukon than in the NWT poison program areas, and that they did not constitute a hazard to game populations. Since that time, the use of poison has gradually declined. In 1972, the use of poison was restricted. In the 1960s, trapper harvests averaged 54 per year and bounties (in effect from 1959 to 1971) were paid on an average of 109 wolves. In the 1970s, trapper harvests increased to 129 per year. During this period non-residents took an average of 27 wolves per year, compared to the less than 10 wolves taken annually by this group since 1950. Wolf harvests by resident hunters are uncertain but are estimated to be 30–50 annually. Aside from Fuller's statistics on wolf harvests per bait station, there have been no comprehensive inventories of wolf abundance in the Territory.

Variation in wolf densities is expected, as there are marked differences in prey availability in different areas of the Territory. Evaluation of the influence of prey diversity and abundance on wolf densities has not been attempted. The extent of disease-caused variation in Yukon wolf densities is unknown, although Bergerud (pers. comm.) has speculated that disease may now be reducing the numbers of wolves that interact with the Porcupine Barren-ground Caribou Herd. Reports of rabies affecting wolves on the Alaskan north slope (Chapman 1978) and reports of distemper outbreaks in Southwestern Yukon have been received, but the extent of these diseases is unknown. Carbyn (1982*a*) discussed the influences of disease in a southern population of wolves. The effect of man-caused and natural influences on wolf densities, distribution, and biology is unknown.

Wolves were until recently protected from trapping and non-native hunting within two preserves: the Fishing Branch Game Preserve (3850 km^2) and the Peel Game Preserve (5950 km^2). Very few wolves were taken by natives in these areas. Protective status, however, was extinguished in the recently revised Wildlife Act (1982). Wolves receive complete protection in the Kluane Game Sanctuary (6860 km^2), the McArthur Game Sanctuary (1750 km^2), and Kluane National Park (21 760 km^2). In total, these areas constitute 5.7% of the Yukon's land area.

Throughout the rest of the territory, Yukon law (Game Ordnance 1958) classifies wolves as "big game". Wolves can be legally taken by licensed trappers or shot by resident and non-resident hunters during the period 1 August – 31 March. No seals are required and

Figure 1
The location of preserves, parks, sanctuaries, and livestock (predominantly horse) wintering areas in the Yukon Territory

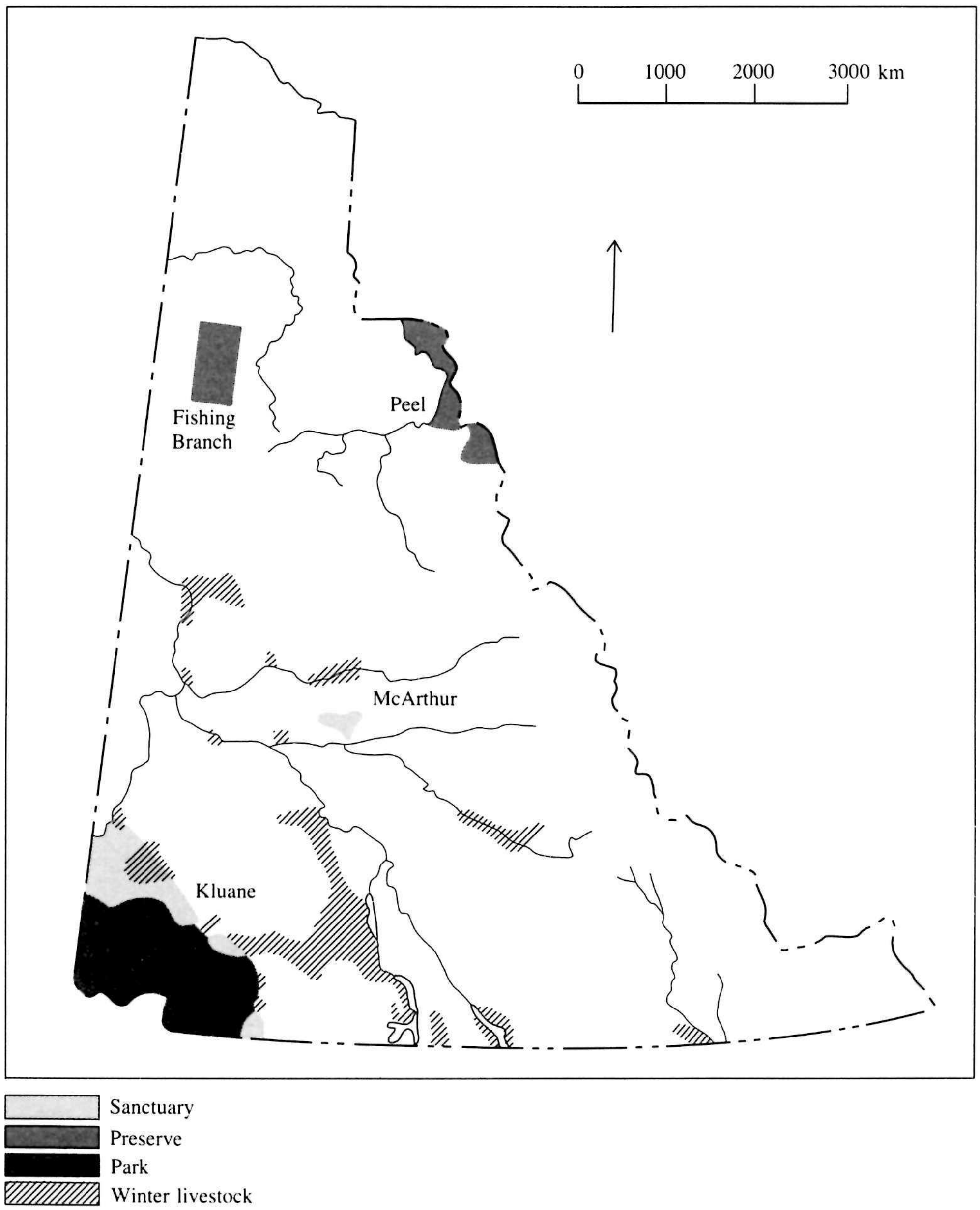
there is no limit on the number of wolves that can be taken per hunter; this is now under review. Regulations prohibit aerial hunting and the use of poison by the public.[1] The relatively low vulnerability of wolves to traditional hunting and trapping methods offsets the effect of these liberal open seasons and bag limits.

Livestock-related wolf problems are not severe in the Yukon because there are only a few hundred horses, less than one hundred cattle, and no free-ranging sheep or goats (Fig. 1). Illegal poisoning in horse wintering areas occurs occasionally, but the number of wolves killed is believed to be low (Hoffman, pers. comm.). Where complaints are received that healthy, enclosed livestock are being injured by wolves, the Government or the Department of Renewable Resources will attempt to remove the wolves by aerial hunting, poisoning, or trapping. Fewer than 10 wolf control actions are conducted annually (Yukon Dep. Renewable Resour., Annu. unpubl. rep.).

No wolf population reduction programs to benefit ungulate populations are in effect.[1] Such actions would only be considered in the future if declines in prey species were well documented and if wolf predation was conclusively identified as the most significant cause. Given the present state of knowlege of ungulate population status, wolf control programs to benefit prey populations are unlikely in the near future.

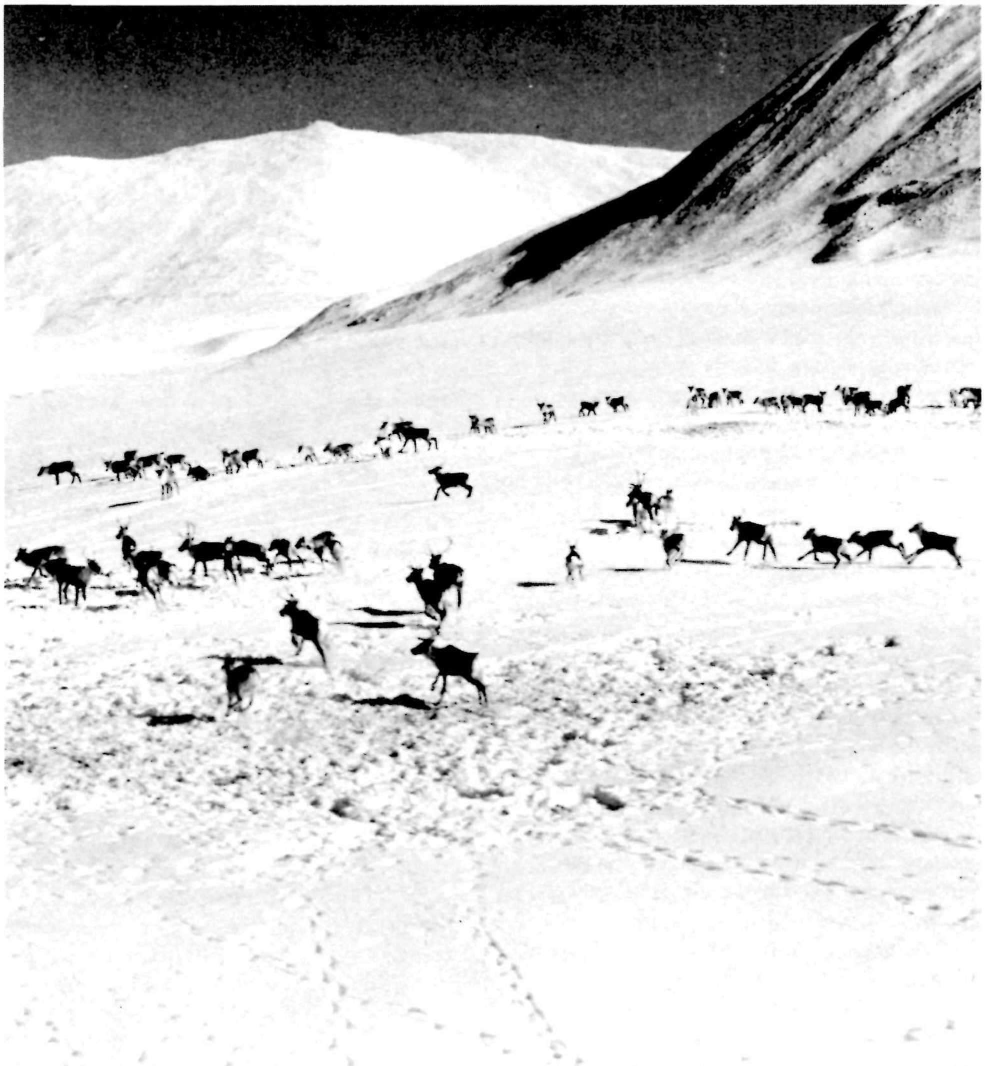
In the territorial economy, wolf harvest revenues and management costs are insignificant. Wolves annually contribute about $9200, or 1% of the total value of raw furs exported from the Yukon. Many resident and non-resident hunters desire wolf pelts, but harvests are low. Non-residents are charged a $75 trophy fee when they take a wolf but at present wolves constitute only 4% of the non-resident harvest. Costs to the government and the public arising from wolf problems are low; rarely do they ex-

Figure 1



Since this paper was written, wolves have been killing livestock on the outskirts of Whitehorse. This, together with local demands for wolf control to increase moose numbers, created a public controversy and precipitated renewed demands for wolf poisoning. Initial plans for a more widespread program in the winter of 1982/83 were curtailed.

Caribou are important in the food habits of wolves in northern areas. Predation on caribou has become a much debated issue and, within the context of the controversy, places man's consumptive interests in conflict with predators (photo: CWS)



ceed $2000 annually. Livestock owners are not compensated for stock losses caused by predation. Wildlife management costs for the wolf are less than $5000 annually.

The limited attention wolf management currently receives in the territory is due in part to the lack of data and the financial limitations, and in part to the species' low priority relative to other big game and fur bearing animals. The inventory and regulation of wolf harvest by hunters and trappers is currently under review for improvement. It is expected that wolves will receive increased attention as the ungulate data base and harvest pressure increase, or if wolf pelt values or livestock numbers increase.

Acknowledgements

Thanks are extended to R. McAndless and Yukon Archives staff for assistance in the historical review and to B. Slough and W. Kale for editorial assistance in the preparation of this paper.

Historical and current perspectives on wolf management in Alaska

Samuel J. Harbo, Jr.
Frederick C. Dean

Figure 1
Game management units in Alaska

1. Abstract

The significant socio-political events and conditions relating to wolf control and management in Alaska since 1900 are summarized. Indiscriminate killing, characteristic of the early 20th century, was supplemented with territorial bounties. Following World War II a federal control program was developed with emphasis on poisons and aerial hunting. Statehood in 1959 coincided with increasing concern for wolf populations; formal control was discontinued except around domestic livestock. The 1970s were characterized by sharp increases in wolf numbers, declining ungulate populations, state-initiated control operations, and intense complex litigation. Each of these phases has been covered in considerable detail.

2. Introduction

Wildlife management programs result from complex relationships between human values and desires and are not based solely on the biological components of resource systems. Consequently we have focused on the historical and socio-political framework. A review of the biological aspects of at least one series of recent wolf control actions is currently being prepared by the Alaska Department of Fish and Game (ADF&G). The present paper gives the outline of this review, but those who require greater detail will have to read extensively in the many documents we have referred to.

The authors prepared the following review, presented as an annotated chronology, to highlight agency programs, public attitudes, and some of the factors influencing them. A great deal of information was obtained from annual reports submitted by the federal Branch of Predator and Rodent Control (BPRC), Alaska District, of the US Fish and Wildlife Service (USF&WS) for the fiscal years 1950–65. For economy of space, specific references to these reports as well as citations for commonly known information are excluded. Alaskan geographic names are referenced to appropriate Game Management Units (GMU) shown in Figure 1. Material in sections entitled phases I to IV are brief thumbnail sketches of events from the more distant past. Phase V deals with recent events.

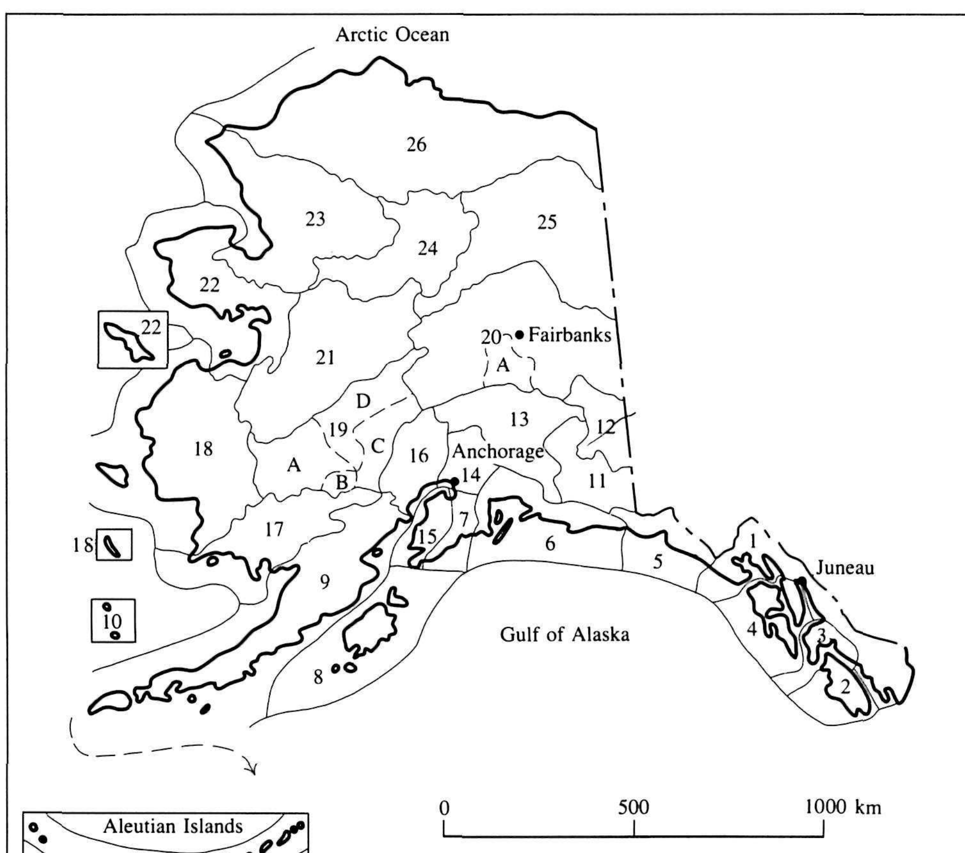
3. Phase I — Indiscriminate wolf control during the early 20th century

During the early white settlement and mining period there was little if any organized government wolf (*Canis lupus*) control; the public generally considered wolves as competitors. Private control efforts were widespread and quite possibly effective over large areas.

1900. There was extensive market hunting in interior Alaska because of the large number of miners. Dall sheep (*Ovis dalli*) were sold in Fairbanks (GMU 20) by the hundreds. Sledgeloads of moose (*Alces alces*) were dumped by the trail to town when outbound hunters reported that the price had dropped severely. Market hunters commonly poisoned the remains of carcasses in order to kill wolves. Wolf populations were reportedly low.

1903. The Camp Fire Club of America (CFCA) was formed. Influential members of the scientific community, such as Ernest Thompson Seton,

Figure 1



Note: Copies of ADF&G Federal Aid Wildlife Reports and other unpublished reports may be obtained from the Alaska Dep. of Fish and Game, Subport Building, Juneau, AK 99801 or from the Fish and Wildlife Reference Service, Unit I, 3840 York St., Denver, CO 80205.

William T. Hornaday, and Gifford Pinchot lobbied strongly on Alaskan parks and wolf control (Belt 1956).

1914. The US Biological Survey was authorized by Congress to conduct experiments and demonstrations on animal control, including wolves (Young and Goldman 1944).

1915. The first federal appropriation was passed specifically for Biological Survey control work on federal lands (Young and Goldman 1944).

1915. The first territorial legislature passed a $10 wolf bounty (Lensink 1959, in ADF&G Annu. Rep. for 1958). Bounties were paid continuously until 1968 (later in some areas), well after statehood.

1917. Congress established Mount McKinley National Park (between GMUs 13 and 20) after heavy lobbying by CFCA and others.

1926. In one of few recorded counts from the period, Frank Glaser, a guide who eventually became an expert federal wolf hunter, tallied 5000 Dall sheep in a 240-km stretch of Alaska Range just east of McKinley Park (BPRC 1953, unpubl. rep.). This indicated an abundance of sheep.

1936. William Beach reported few sheep in Mount McKinley National Park compared to his observations in 1925 (Belt 1956). Cahalane (1946) described considerable evidence relating the sheep decline with severe winters.

1937–47. CFCA urged wolf control in Mount McKinley National Park because of low sheep numbers (Belt 1956). The National Park Service initially responded by starting Adolph Murie's study of wolves and sheep in the Park. The US Biological Survey's pre-World War II wolf control work in Alaska mostly concerned reindeer (*Rangifer tarandus*) herds.

1944. Murie (1944) concluded: "The wolf is the chief check on the increase of the Dall sheep in Mount McKinley National Park .... wolves prey mainly on the weak classes of sheep .... [such predation indicates] normal predator–prey adjustment....". Differences of views on park management flared. Belt (1956) commented: "Murie's report failed to outline any emergency policy. It was an elaborate treatise on animal behaviorism. The only ... indications of a policy were in favor of the wolf ...".

4. Phase II — Organized federal wolf control during territorial days

The federal wolf control program became one of the dominant aspects of wildlife management in Alaska. Biological information on predator–prey interactions was still scarce and public attitudes were still largely anti-wolf.

1945–46. CFCA drafted and had introduced into Congress Bill HR-5401, directing rigid control of wolves in Mount McKinley National Park (Belt 1956). The National Park Service reluctantly decided to kill up to 15 wolves (about 50%) on the Park sheep range before passage of the Bill (Cahalane 1946).

1948. The BPRC expanded its operations in Alaska. The acquisition of a Super Cub aircraft the following year allowed intensive aerial hunting.

1950. The BPRC's national policy contained the statement: "[On wilderness areas] ... where predators do not jeopardize livestock or game on or near the area, the Fish and Wildlife Service does not advocate or practice predator control" (Presnall 1950). However, operations in Alaska left room for argument about the interpretation of "wilderness", "jeopardize", and "practice".

1951. Mount McKinley National Park wolf control ended; probably fewer than 12 wolves had been shot, snared, or trapped during the 6 years since Bill HR-5401 was introduced (W. Nancarrow, pers. comm.).

1952. Territorial Sportsmen Inc., a Juneau (GMU 1) club, began continuing financial support of local BPRC control work. "Operation Umiat" established three two-man hunting teams with aircraft, which covered approximately 65 000 km^2 on the north slope of Brooks Range (GMU 26) between 21 March and 8 May. Aerial hunting and poison baits killed 259 of the 334 wolves seen (BPRC 1952, unpubl. rep.; Leveque 1954). National publicity produced substantial adverse reaction. "Umiat" probably intensified the debate between biologists and control agents in Alaska regarding the need for widespread control. A. Starker Leopold and F. Fraser Darling, sponsored by the Conservation Foundation, toured Alaska during much of the summer; they saw most aspects of USF&WS and Alaska Game Commission operations. BPRC restricted poison stations in southeast Alaska (GMUs 1–4) to the period 15 October – 31 March as protection for bears. Baits were often set on lakes by aerial drops (Fig. 2).

5. Phase III — Transition preceding state management

During the 1950s there were increasing differences of opinion between many biologists and most control agents about the necessity of wolf control. Public attitudes were slowly becoming pro-wolf, based largely on the wilderness symbolism of wolves and their rarity elsewhere; reaction against the use of poison increased.

Wolf control was becoming more oriented toward specific situations. Bounty systems were being questioned more frequently although many people justified them as a form of rural welfare.

1953. BPRC modified the "coyote getter" (cyanide bait gun) for use on wolves; in spite of problems, this became the standard control method in summer. A BPRC staff of six or seven field men covered the territory. Leopold and Darling (1953) discounted the significance of predation in unhunted or lightly hunted moose and caribou populations and urged local assessment before implementing wolf control. Fire was considered a major factor in the reduction of caribou winter ranges, and predation was recommended as one tool for regulating caribou numbers.

1954. Heavy reindeer losses to wolves were documented for the Kotzebue area (GMU 23).

1953–54. In southeast Alaska, the BPRC agent stated he was concentrating on specific problem areas in contrast to the scattered approach previously used.

> It has to be admitted that after many years of bait station work on the beaches of southeastern Alaska nothing was learned of wolves except that they do come to the beaches and will be killed if they eat lethal baits (BPRC, unpubl. Annu. Rep. FY1954).

Three teams of private aerial hunters shot about 200 wolves in arctic Alaska; caribou

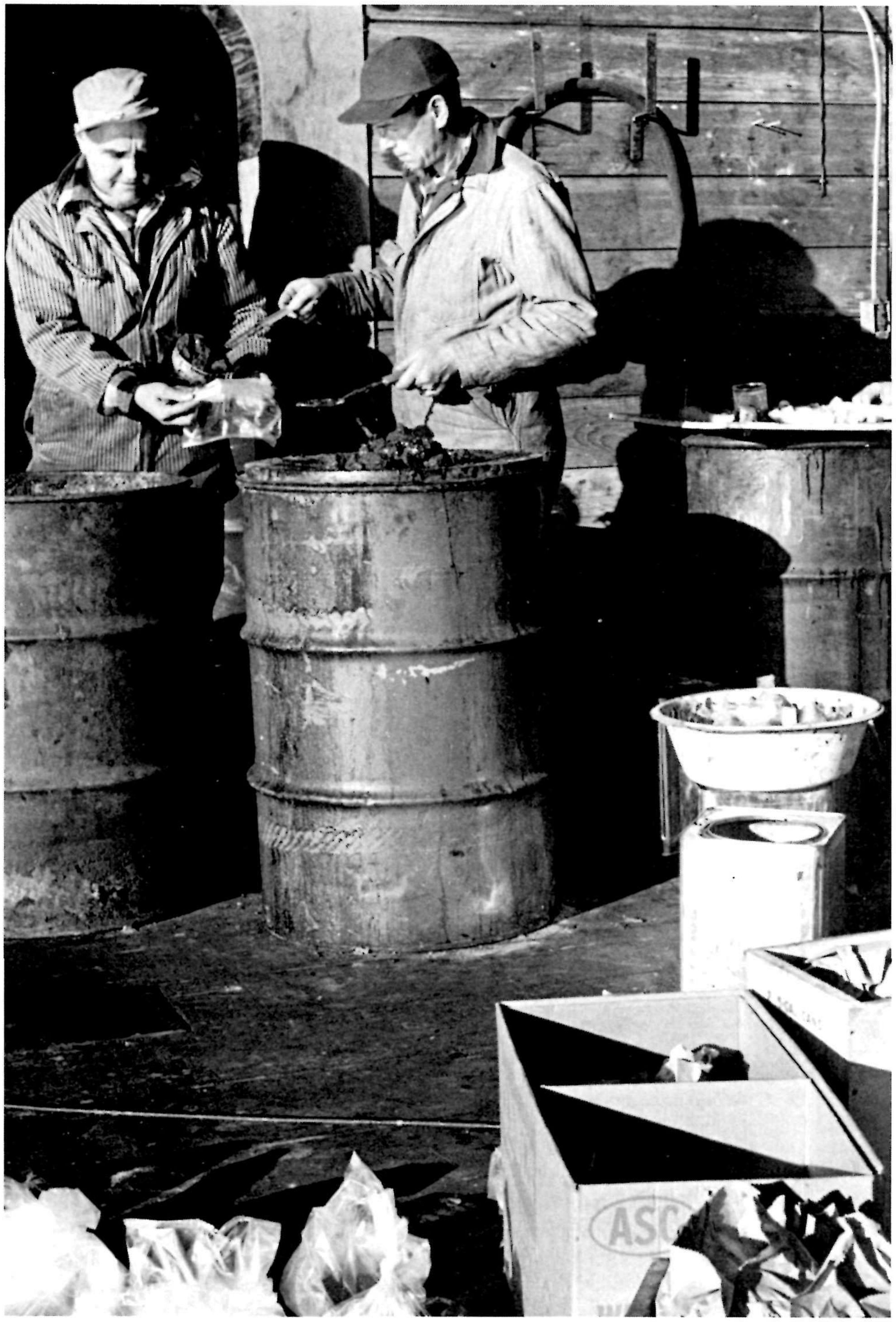
Figure 2
A USF&WS biologist and assistant examine wolf carcasses from a poison bait station near the interior village of Northway in the early 1950s. This scene closely parallels those seen at the time in coastal southeast Alaska (photo courtesy of USF&WS)

killed annually by Iñupiaq in the Arctic were estimated at 15 000 (Woolford 1955, USF&WS, unpubl. rep.).
1955. Five teams of aerial bounty hunters shot more than 90 wolves in 6 weeks in northern Alaska.
1956. Crisler (1956) concluded that there was significant selection by wolves for weak and crippled caribou. Wolf populations were generally increasing throughout Alaska except on the Alaska Peninsula (GMU 9). Bounty hunters took over 200 wolves in the Kotzebue region.
1957. The Secretary of the Interior closed the Nelchina Basin (GMU 13) to the taking of wolves to permit research on undisturbed predator–prey interaction; biologists felt caribou were nearing the carrying capacity of the range and thus increased predation was desirable.

The Territorial legislature transferred the Co-operative Predator Control Program from the Treasurer's Office to the new ADF&G. A new co-operative agreement was signed: BPRC was to be in charge of control and ADF&G in charge of investigations. BPRC admitted that predator–prey interactions were not well understood, and that wolf propulations were increasing in spite of the control program.

A private aerial bounty team killed 118 wolves in the first significant hunt in the forested interior.

Figure 3
Seal blubber baits (3000 L) being prepared with strychnine in the 1950s (photo courtesy of USF&WS)



Over 200 dead moose, presumed wolf kills, were reported from the Koyukuk Valley (GMU 24); the spring snow had a hard crust, easing wolf travel.

BPRC was to decide the priorities, under its predator priority rating system, of three factors: human use of the area; predator and prey population levels; and range conditions. Strychnine was the common poison used (Fig. 3).

1958. Arctic Wild, a book by Crisler (1958), fostered much pro-wolf sentiment.

More than 1500 wolves were killed in the previous 6 years in GMU 26, which includes the Operation Umiat area. It was only in this year that biologists discovered the location of the calving grounds of the Western Arctic Caribou Herd, which uses parts of GMUs 23, 24, and 26. This late discovery is an example of the general lack of biological knowledge of Alaska wildlife. The total cost of wolf and coyote bounties in Alaska up to 1958 was over $1.5 million.

1959. ADF&G analysis of bounty systems stated (Lensink 1959, ADF&G Annu. Rep. 1958):

> Predator control is a necessary and valuable tool of wildlife and fisheries management. To be most useful this tool should be applied at the right place, at the right time, and in the most efficient way possible. All of these requirements can be met by a carefully designed program, but none of them is achieved with a bounty system.

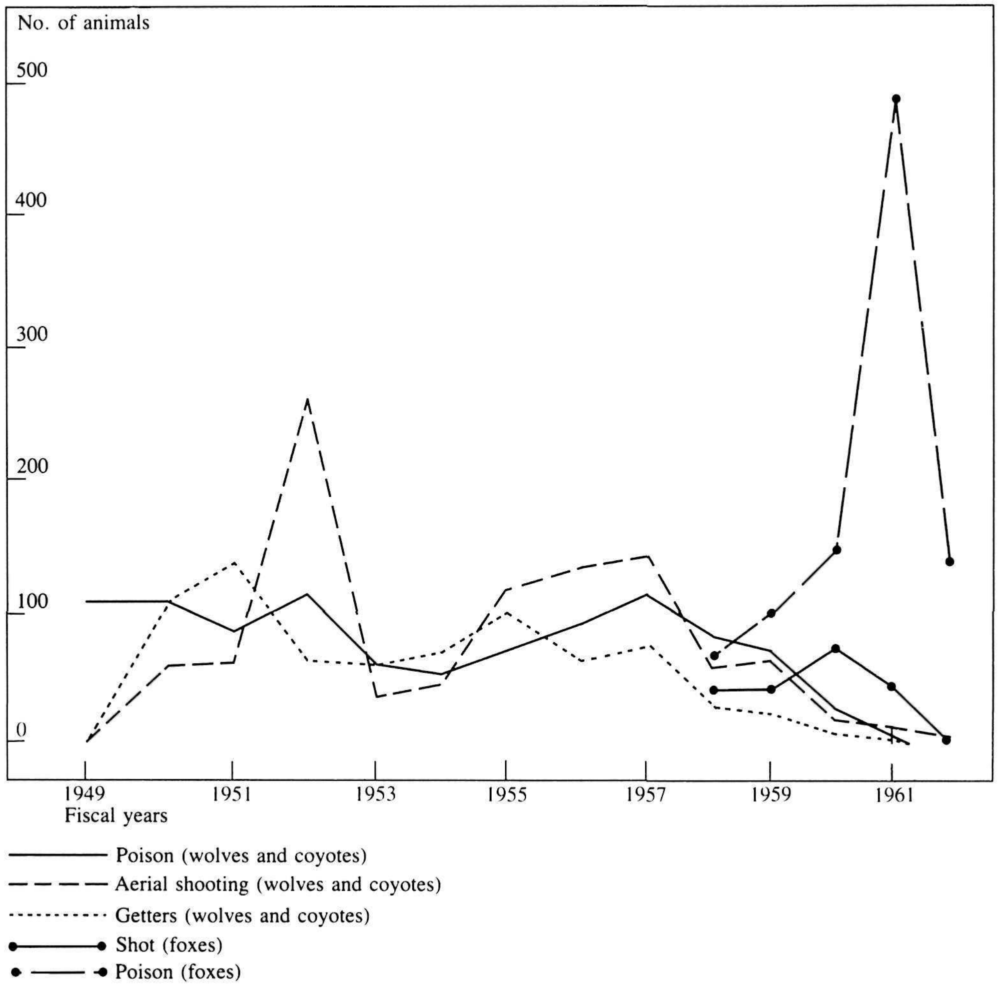
BPRC reopened the Kotzebue station, particularly for wolf control around reindeer herds.

ADF&G began intensive studies on wolf carcasses. Burkholder (1959) reported no discernible prey selection in his Nelchina study.

The Predator Control Committee of the Tanana Valley Sportsmens Association failed to reach agreement, after many interviews and two winters of study, on the need for wolf control or the methods to be used (Tanana Valley Sportsmens Association, 1959, Fairbanks, AK, unpubl. rep.).

Figure 4
Methods used by the federal Branch of Predator and Rodent Control to remove predators in Alaska

Figure 4



6. Phase IV — State assumption of predator management

Control of predator management was assumed by the State of Alaska. Increased game, trophy, and aesthetic status for the wolf was widely promoted; at the same time public interest in environmental concerns grew rapidly.

1960. On 1 January the new State of Alaska assumed authority over decisions concerning resident wildlife and whether to conduct control. Game biologists felt it advisable to reduce both the Arctic and Nelchina caribou herds because of deteriorating range conditions.

Some polar bear guides, responding to the public's changed perception of wolves as trophies, began introducing their clients to aerial wolf hunts following the bear hunts.

BPRC wolf control was restricted to reindeer range. By local agreement at Fairbanks, ADF&G decreed: (a) "getters" were to be used only in emergency situations, (b) bait stations were to be checked every 10 days, and (c) wolf carcasses should be recovered for biological study whenever possible. ADF&G required reduced wolf control on Tanana Flats (GMU 20) because the moose population was large and generally inaccessible; wolf numbers there were increasing slightly. In another area four wolves were released on Coronation Island (GMU 3) as an experiment with wolf–deer relations (Merriam 1964).

1961. The Alaska Big Game Trophy Club actively promoted trophy status for wolves taken after "fair chase". BPRC reduced their staff in Alaska to three permanent employees and ADF&G assumed responsibility for the Nelchina wolf study. Figure 4 summarizes BPRC control effort through 1962. Numbers of wolves were reported to be increasing generally except in arctic areas. Rausch presented a review paper on wolf management at the Alaska Science Conference (Rausch 1961).

1963. Mowat (1963) published a largely unsupported account of wolves; he discounted the significance of wolf predation on caribou. The book became a bestseller and generated widespread sympathy for wolves.

The Alaska Board of Fish and Game classified wolves both as big game and furbearers. The Board also promulgated regulations imposing a limit of two wolves taken by aerial bounty hunting in arctic Alaska.

1964. A study of Coronation Island showed a drastic reduction in the number of deer as a result of the wolves released there in 1960 (Merriam 1964).

The report of the Leopold Committee on federal predator control policy, given at the North American Wildlife Conference, recommended the establishment of an advisory board, the need for internal reassessment, and explicit criteria pertaining to the legal control of poisons, etc. (Leopold 1964).

Rausch (1964) summarized progress in wolf management and research in Alaska since 1959 and reported low wolf productivity in arctic Alaska.

1965. The Secretary of the Interior adopted the Leopold Committee report as policy. A study of wolf predation on moose on Isle Royale reported that wolves were strongly selective of calves and older adults and that, in general, predation was maintaining the moose herd within food limits and in good condition (Mech 1966). The study further promoted the positive image of the species.

1966. Gordon Haber began studies in Mount McKinley National Park; these led to an ecosystem model (Haber 1977) and hypotheses which he later invoked during a long debate with ADF&G.
1967. It was stated in the proceedings of a symposium on wolves that wolves in Alaska showed strong reproductive performance and that pup mortality was the cause of fluctuating populations (Rausch 1967).

A new federal policy on the control of damage by animals emphasized co-operation with states and landowners; operational guidelines appeared restrictive but essentially permitted most earlier practices (Anon. 1967, 1979).

7. Phase V — Active wolf control by state and court intervention

The next section deals with the last decade in greater detail. The various developments discussed in phases I–IV concerning changes from near-colonial status to statehood, increases in ecological understanding, changing emphasis from consumptive to non-consumptive interest in wildlife, and the development of legal processes to support public concern about environmental problems should be kept in mind.

During this decade, bounties were abolished, tight controls on aerial hunting were imposed, state biologists' attitudes toward wolf control changed, wolf control resumed, and the courts became involved.

In 1968 the Alaska State Legislature granted the Board of Fish and Game the authority to abolish bounties on an individual GMU basis. The Board did so in all except some GMUs in southeast Alaska, where a bounty persisted for several more years.

In 1971 US Congress enacted Public Law 92-157, known as the Airborne Hunting Act, which prohibited use of aircraft in hunting except under state permit. Alaska chose to continue issuing aerial hunting permits through the winter of 1971/72, which infuriated those who thought the federal law had completely banned such hunting. Partly in response to public outcry, the ADF&G Commissioner halted further issuance of aerial wolf-hunting permits.

Some groups bitterly denounced the cessation of aerial hunting. The Interior Wildlife Association, a newly formed organization whose goals were cessation of cow-moose hunting and reinstitution of wolf control, published the first issue of Alaska Wildlife Digest in the latter part of 1972. The Digest's articles attacking the ban on aerial permits matched the fervour of the arguments that only months earlier had castigated ADF&G for continuing permits. Thus, one segment of society elevated wolves to a value above that of other animals, while another seemed to place only negative values on wolves. A report on predator control and bounties in Alaska briefly summarized the situation that prevailed during the early years of statehood (Anon. 1972).

In 1973, the Board of Fish and Game and ADF&G published a series of policy statements made necessary by increasing human population and resource development (ADF&G 1973, unpubl. rep.). They included the statement that:

> Traditionally, game management has emphasized maximum production of ungulates for man's use .... [but] aesthetic or nonconsumptive uses are gaining prominence in resource management.... Wolves ... will survive if ungulates are managed successfully, providing they receive a minimum of protection from humans. In this sense wolves can be considered an indicator of our stewardship of Alaska's land. Land areas supporting substantial populations of wolves have not been severely abused by man....
> Whenever substantial conflicts arise between humans and wolves over the use of prey, the wolf population will be managed to minimize such conflicts. The various recreational and aesthetic values of the wolves will be considered equally with similar values of the prey species in the final management decision.

Many significant reductions in the sizes of important prey populations had occurred concurrently with increased protection afforded wolves from 1969 to 1972. Some examples are: the Nelchina Caribou Herd decreased from approximately 70 000 animals in 1962 to less than 8000 in 1972 (Bos 1975); the moose population in GMU 20A decreased from more than 10 000 in 1965 to about 2900 in 1974 (Coady 1976*a,b*; ADF&G 1979, unpubl. issue paper 79-07); and the Steese-Forty Mile Caribou Herd decreased from 40 000 in the 1960s (Skoog 1968) to approximately 5000 by 1974 (Davis *et al*. 1975, ADF&G Fed. Aid Wildl. Rep.). The coincidence of prey population declines and increased protection (and populations) of wolves increased the clamour to reduce wolf numbers, although other factors such as winter mortality and the increased take by humans were also clearly responsible for the declines.

By 1973 Alaskan wildlife managers had data from several depressed prey populations that seemed to implicate wolves (Rausch and Hinman 1975). In southeast Alaska for example, the abundant deer populations of the late 1950s and early 1960s declined by the early 1970s to low levels on all major islands where there were wolves, but persisted at moderate levels on major islands without wolves (Rausch and Hinman 1975, Olson 1979).

The decline of the GMU 20A moose population, a population now hunted mainly by Fairbanks residents using motorized surface vehicles seemed to be caused by weather (Fig. 5), harvest by humans (Fig. 6), and predation by wolves (Coady 1976*a,b*). Although the GMU 20A moose population had declined by 1971 to well below the carrying capacity of the habitat (Coady 1976*a,b*), poor calf and yearling survival followed the mild winters of 1971/72, 1972/73 and 1973/74 (McKnight 1974, 1975, and 1976, ADF&G Fed. Aid Wildl. Rep.; Coady 1976*a,b*). By 1973 the data convinced wildlife managers in Alaska that wolves, at the very least, contribute to declines in prey populations and help keep them low. By 1974 the managers reached a conclusion that was unthinkable 10 years earlier: in order to rehabilitate the depressed GMU 20A moose population so that desired levels of harvest by humans could be reinstated in a reasonable time, wolf control should be undertaken. ADF&G officials recognized public controversy would ensue,

Figure 5
Estimated moose abundance and yearlings per 100 cows in GMU 20A moose populations (courtesy of ADF&G)

Figure 6
GMU 20A moose harvest from 1963 to 1975 (courtesy of ADF&G)

Figure 5

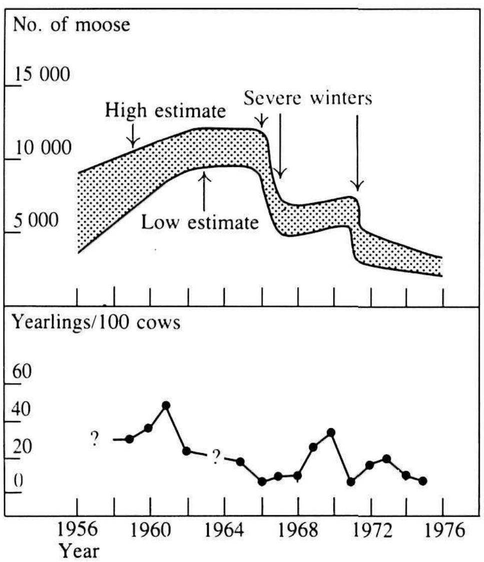
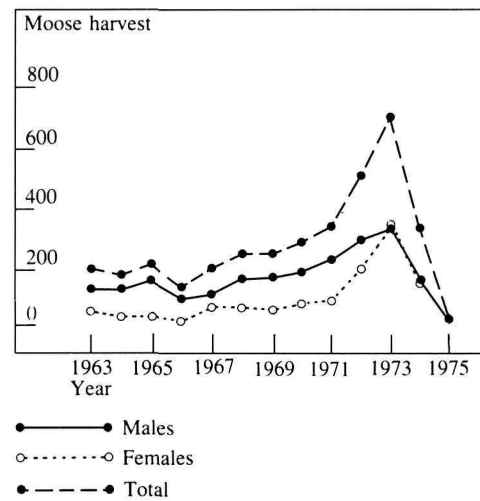


Figure 6



requiring a cautious and considered approach on their part. In early 1975 a recommendation was submitted to the Board of Fish and Game for approval.

Using limited survey data, ADF&G biologists estimated the GMU 20A wolf population at about 175 (Rausch and Hinman 1975). Fairbanks residents believed wolves were numerous locally because during the winters of 1974 and 1975 30–35 dogs were killed by wolves at outlying homes in the Greater Fairbanks area. There was increased concern for the safety of school children walking to and from school buses during the dark, but in fact there were no instances of wolves attacking humans.

In February 1975 the Board approved a plan to hire private pilot-gunner teams to shoot wolves, directing the Commissioner to implement the plan immediately. A prompt law suit filed on 18 February 1975 in the Alaska Superior Court, Third Judicial District, by the Fairbanks Environmental Center, Friends of the Earth, and several individuals, resulted in an injunction on 3 March 1975 halting the program. The suit was resolved in favour of the plaintiffs, not on the grounds that the control activity was biologically inadvisable, but on a technical violation of an Alaskan statute involving promulgation of regulations. Rausch and Hinman (1975) reported on the managers' perception of the wolf control controversy.

The acrimonious public controversy over wolf management in Alaska prompted the Commissioner, in a letter dated 17 June 1975, to request the National Audubon Society to conduct an impartial review of wolf management policies in Alaska. The Society confirmed their willingness to undertake such a review, specifying the funding needed. At the same time, ADF&G continued with its wolf reduction plans.

In spring 1975 the Alaska Legislature split the Board of Fish and Game into two seven-member boards, the Board of Fisheries and the Board of Game. In December 1975, ADF&G submitted a modified wolf control plan to the Alaska Board of Game (following the legal rebuff the previous March). Moose investigations in GMU 20A during 1975, following another favourable winter, revealed continued low calf and yearling survival with the depressed population either stable or still declining (McKnight 1976, ADF&G Fed. Aid Wildl. Rep.).

GMU 20A was not the only location in which officials felt action had to be taken. In GMU 5 a small moose population, important to local hunters, was subjected to significant wolf predation after severe winters and possible over-exploitation by humans had reduced the herd (Rausch and Hinman 1975). The human harvest of moose had declined from more than 300 annually in 1968 and 1969 to only 147 in 1973 (McKnight 1975, ADF&G Fed. Aid Wildl. Rep.). Wolf reductions were to be recommended if the monetary resources of ADF&G permitted.

A third project planned by ADF&G in 1975 was to carry out research on wolves in relation to moose in GMU 13, in order to learn more about wolf–prey ecology in Alaska. The project necessitated complete extirpation of wolves (about 45) in an 8000 km^2 experimental area, and subsequent comparison of moose (calf and yearling) survival with that in a nearby area where wolves had not been removed. A study on food habits and ecology was already in progress in those two areas, using radio-collared wolves; the study was supported by federal Pittman-Robertson funds (Stephenson 1978, ADF&G Fed. Aid. Wildl. Rep.). The new ADF&G project was reviewed and approved by USF&WS officials for federal aid. The Board of Game approved all three projects (GMU 20A, GMU 13 control study, and GMU 5) in December 1975, directing ADF&G to use fixed-wing aircraft and helicopters, with only ADF&G personnel participating. This last directive enabled the operation to be monitored and closely regulated in order to alleviate public concern about numbers and locations of wolves taken. The Board specified that wolf reductions in GMUs 5 and 20A should not exceed 80% and that the objective should be a ratio of 1 wolf to 100 moose. This ratio was based on observations that moose populations with ratios of 1 wolf to 20 or fewer moose declined (ADF&G 1979, unpubl. issue paper 79-07). Therefore it was considered that a population with a 1:100 ratio should surely increase. The wolf reductions in the three GMUs were tentatively scheduled to run for 3–4 years, but the GMU 5 project was never implemented because of inadequate funds.

Meanwhile ADF&G and the National Audubon Society had finalized the terms of the review of Alaskan wolf management policies.

However, in view of the above actions by the Board, the Society's Executive Vice-President, in two letters to the Commissioner, dated 16 January and 4 February 1976, expressed concern that the credibility of the review would probably be severely damaged. He reasoned that the public might gain the impression that "... the National Audubon Society consented to or gave tacit approval to ..." the control programs, and that "... our study team would be handicapped in its search for facts and unbiased opinion in the present atmosphere of emotionally charged controversy". Unless ADF&G cancelled the hunts, the Society would withdraw from the contract. The Commissioner responded in a letter on 9 February 1976 by stating, in part:

> There was never a suggestion much less a commitment that any of our programs ... would be put on ice until the ... study had been concluded. We are certainly not attempting to polish our image by associating with the Audubon Society and ... our motives are sincere in seeking an objective third-party assessment of the wolf situation in Alaska.
> If such an endeavor at this time would unavoidably implicate the Audubon Society in issues that could only prove damaging to your conservation objectives and credibility, then I can certainly understand the decision to abandon the study that we had contemplated.

The control programs proceeded, and the Society withdrew from the contract.

Meanwhile efforts to delay or stop the control programs were initiated. National television editorials generated a great deal of attention: ADF&G had to contend with substantial misrepresentation. Thousands of protesting letters were addressed to the Governor or ADF&G.

A calendar of the most important events follows:

5 Jan. 1976. A letter was sent by the Defenders of Wildlife to the Secretary of Defense demanding an Environmental Impact Statement (EIS) before allowing control by ADF&G on the Department's lands in GMU 20A.

19 Jan. 1976. The USF&WS suspended funds for the wolf reductions in GMU 13. However, the State decided to continue the project using State funds.

22 Jan. 1976. The Deputy Assistant Secretary of Defense requested certain information about control programs and officially requested that the programs not be implemented on the Department's lands until further notice. The State acquiesced.

23 Jan. 1976. Defenders of Wildlife *et al.*[1] filed suit against the Secretary of the Interior in US District Court for the District of Columbia (DC) claiming that an EIS was needed for the GMU 20A project. A preliminary injunction was requested.

26 Jan. 1976. Preliminary injunction for GMU 20A was denied by the DC judge. Defenders of Wildlife *et al.*[2] filed suit against ADF&G and several officials in District Court for Alaska claiming that an EIS was needed for the GMU 13 control study. An injunction was requested.

28 Jan 1976. A temporary restraining order was issued by the District Court judge in Alaska on the GMU 13 control study.

30 Jan. 1976. The Director, Bureau of Land Management (BLM) asked the Governor of Alaska to suspend wolf hunts in GMU 20A pending a resolution of the question raised in District Court in DC of BLM's management responsibility. The State acquiesced.

6 Feb. 1976. The Assistant Director of the BLM sent a memorandum to the State stating that the point raised on 30 January had been resolved. The State could, and did, continue the GMU 20A hunt.

17 Feb. 1976. Defenders of Wildlife *et al.*, in their suit in Alaska District Court, amended the complaint to include the Secretary of the Interior and the Director of USF&WS as defendants.

25 Feb. 1976. The District Court judge in DC ruled against Defenders of Wildlife *et al.*, stating that no EIS was required for GMU 20A.

27 Feb. 1976. Defenders of Wildlife *et al.*, in their suit in the Alaska District Court, further amended their complaint to include GMU 20A (designated Count II; Count I is the GMU 13 complaint) and unsuccessfully requested a temporary restraining order to stop the GMU 20A hunt.

8 Mar. 1976. The District Court judge in Alaska ruled that an EIS was not needed in the GMU 13 control study. He denied the permanent injunction relief requested and dismissed Count I.

9 Mar. 1976. Defenders of Wildlife *et al.* filed notice of appeal against Count I decision.

31 Mar. 1976. A telegram from the Office of the Secretary of Defense cancelled his request for temporary suspension of control programs on Defense lands.

5 Aug. 1976. Defenders of Wildlife *et al.* appealed the decision of the Alaska District Court to the Court of Appeals, Ninth Circuit.

13 Sept. 1976. The Alaska District Court granted ADF&G's motion for summary judgement of Count II. Count II was dismissed.

22 Aug. 1977. The Court of Appeals, Ninth Circuit, reaffirmed the Alaska District Court's decision of 8 March 1976.

The timing of these events gains meaning when it is realised that the short daylight period prior to late January, particularly in GMU 20A, and the predictably poor snow conditions after late March severely limit effective wolf control operations. Moreover, the actions relate almost exclusively to the National Environmental Policy Act of 1969 (NEPA), which requires a written assessment of environmental impacts before any major action by a federal agency can be undertaken.

The actions by the Secretary of Defense and the two court cases established several important points. The action regarding the Defense lands clarified that the State did have manage-

[1] Natural Resource Defense Council, Inc.; Animal Protection Institute; Int. Fund for Animal Welfare — USA; The Humane Society of the US; the Fund for Animals; Animal Welfare Institute; The Wild Canid Survival and Research Center — Wolf Sanctuary; and 4 private parties.

[2] The Humane Society of the US; Animal Protection Institute; Int. Fund for Animal Welfare — USA; The Wild Canid Survival and Research Center — Wolf Sanctuary; the Fund for Animals; Alaska Field Representative for Friends of the Earth; and 4 private parties.

ment responsibility and authority on such lands. The case in the District Court for DC clarified that a 1968 Memorandum of Understanding between Alaska and BLM did not require BLM approval for a wolf-control project unless poisons were used, hence the project could not be considered a "federal-state program". The case also brought out that the fact of federal land being involved does not by itself make wolf control a "federal action". The judge in the DC case further stated that, "... even if a federal action is involved, ... such action does not constitute major federal action significantly affecting the quality of human environment ...." (criteria specified in Federal Register 1 August 1973.) The Alaska District Court reaffirmed the latter point, finding that killing all wolves in the GMU 13 experimental area would only reduce the entire GMU 13 wolf population by 13%; such reduction "... will not significantly affect the quality of the human environment ..." and hence is not a major action requiring an EIS. The Alaskan judge did not rule on the question of whether the action was a federal one.

One action not resolved to the State's satisfaction was the withholding of federal Pittman-Robertson funds from the GMU 13 control study. Even though the Alaska Court ruled that an EIS was not required, USF&WS did not reinstate the funds. In a 27 January 1976 letter to USF&WS the Chairman of the Board of Game questioned the appropriateness of the cutoff. He also implied an improper use of the EIS requirement when he stated:

> Another major concern is that your recent directive contributes to a practice that in the long run may have serious consequences for all of us. That practice is the increasing use of the National Environmental Policy Act of 1969 in an obstructionist way. That is, if an impending action cannot be stopped on any other basis, demand an EIS. At the very least, the process will delay the action. Using environmental quality legislation in that fashion, particularly in an instance such as ours where our man-made perturbation (i.e. reducing the wolf population in all of Unit 13 by approximately 14%) is of less magnitude than others generated by natural environmental processes (i.e. naturally occurring fluctuations in wolf numbers), will substantially reduce public confidence in such legislation, possibly stimulating proposals to substantially weaken the 1969 Act. I hope that the Fish and Wildlife Service's abrogation of the wolf study is not a correct measure of your willingness to be a party to the obstructionist practice.

Despite the obstacles placed in their path, ADF&G personnel thought they had removed all except two or three of the wolves inhabiting the GMU 13 experimental area (Stephenson 1978, ADF&G Fed. Aid Wildl. Rep.). In GMU 20A, the goal was not achieved; the ADF&G operation removed 66 wolves, 69 others were taken by private individuals engaged in commercial or recreational trapping (ADF&G 1979, unpubl. issue paper 79-07). The post-control wolf/moose ratio of 1:29–40 fell short of the desired 1:100, but did represent a substantial change from the precontrol ratio of 1:13 (ADF&G 1977, unpubl. rep.).

The lack of success at stopping the wolf control operation in court led some groups to seek redress in Congress. Four essentially identical bills were introduced into the House of Representatives during the summer of 1976. The bills specified that the Secretary of the Interior, in co-operation with the states, would make a comprehensive study of the wolf for the purpose of developing "... adequate and effective measures ... to conserve such animals and to insure humane treatment in all cases". The bills also specified that "... a moratorium of all hunting of these animals from aircraf ... and all large-scale killing of these animals, whether for research or any other purpose ..." would stop until the Secretary completed the study and made his recommendation. Congress would be authorized to appropriate $50 000 for fiscal year 1977 and for each of two succeeding fiscal years. The bills were not enacted, undoubtedly due in part to very reasoned and persuasive testimony submitted by the Director of USF&WS on 20 September 1976 at a subcommittee hearing. The Director pointed out that the bills infringed on the rights of states to manage their resident wildlife; the inadequacy of the suggested appropriation was also mentioned. Of special interest to Alaska officials were these segments of his testimony:

> In January of this year we issued notice to the State Fish and Game Department suspending federal funding under the Pittman-Robertson Act of a wolf removal project pending review of the project design which subsequently was determined to be adequate. However funding for this project has not been reinstated....
> As you know, Mr. Chairman, there was tremendous public interest generated over this matter. We are still receiving letters almost daily pleading for preservation of the wolf.... There is ... no evidence that wolves are either declining or in critically low numbers in Alaska. The opposite, however, is true with regard to moose and caribou populations in certain areas of Alaska.

Although the advent of summer curtailed the wolf operation, thus quieting the controversy, there were new developments. Preliminary analysis of the July 1976 aerial surveys of the Western Arctic Caribou Herd indicated that the herd had declined from approximately 240 000 animals in 1970 to about 50 000 in 1976 (ADF&G 1976). The herd represented a critical subsistence resource for rural residents in northwest Alaska, with an annual take of approximately 25 000 animals (ADF&G 1976, unpubl. rep.). ADF&G immediately undertook emergency actions to rehabilitate the herd. As studies suggested that the herd's range was not implicated and that humans and wolves caused most of the mortality (ADF&G 1976, unpubl. rep.; Davis *et al.* 1975, ADF&G Fed. Aid Wildl. Rep.; Doerr 1979), emergency action to reduce the take by both was initiated. ADF&G closed the year-long open hunting season in August, pending development of very restrictive new regulations, and formulated plans for wolf reductions in the herd's winter range. The agency held public hearings in Barrow (GMU 26), Fairbanks, and Kotzebue during early August to obtain public input on management plans. At the 4 August 1976 meeting in Fairbanks, the Alaska Conservation Society recommended the human take of caribou be reduced as much as possible (preferably to zero) and suggested that the current plight of the Western Arctic herd

> ... may be one of those unusual situations where short and long term human benefit, and perhaps even long term benefit to wolves themselves (since wolves depend on caribou) requires that the Department of Fish and Game reduce wolf numbers as a temporary, emergency measure to lessen the decline in the Western Arctic Caribou Herd [see also Weeden 1976].

Some conservation groups outside Alaska did not share those views. In an August news release, the Wildlife Committee, Atlantic Chapter, Sierra Club criticized ADF&G and cited numerous reasons why the control operation should not be undertaken. In addition, the news release contained these suggestions:

> You may well ask what you can do to stop these hunts; all concerned citizens and environmental groups can take the following actions:
> The State of Alaska has recently requested the federal government lift the moratorium on the taking of 9 marine mammals ... now protected under the Marine Mammals Act. Though the populations of these animals have reached somewhat healthy levels ... the State of Alaska, in light of its wasteful and environmentally unsound management of wolves, [should] not be given ... management of these mammals unless Alaska proves it is capable of conservative wildlife management practices such as in regard to its wolf population. Express these views to: Thomas Kleppe, Secretary of Interior ...

The release further suggests:

> We know from last winter's experience that appeals to stop the wolf hunts were met with deaf ears by Governor Hammond of Alaska, the ADF&G and President Ford. This year we are approaching the one political figure we believe to have a deep enough interest in the environment to do something about stopping these perversions of game management. Write to Jimmy Carter asking him to publicly back-up our views concerning the destructiveness of these hunts and their unhealthy environmental character.

The Alaska Conservation Society, through its Vice-President, responded to that news release on 6 October 1976. The response included the following:

> The news release "Alaska Plans Massive Expansion of Aerial Wolf Hunts" issued this summer by your committee is an embarrassment to Alaskan and national conservationists. You use bad facts and — not surprisingly — reach unsupportable conclusions. I hope this letter helps set you straight and can be the basis for a more accurate information program on your part.... We have enclosed some information you should study carefully. Next time you want to make something public about Alaska, please check the facts. We'd be glad to help.

The Board, during the fall of 1976, directed ADF&G to conduct a wolf-reduction program in the high wolf density portions of the Western Arctic herd's winter range, located in GMUs 23 and 24. Again, up to 80% of the wolves in the designated areas were to be removed during the winter 1976/77, but by private hunting teams with permits and not by ADF&G personnel. On learning of the proposed action, legal representatives of the National Resources Defense Council, Defenders of Wildlife, and the Alaska Chapter of the Sierra Club asked the Secretary of the Interior, in a letter dated 11 November 1976, to prepare an EIS prior to any State control activity. They contended that a Memorandum of Understanding of May 1976 between ADF&G and BLM, plus the fact that most lands involved were BLM lands, made BLM responsible for the control action, thus requiring an EIS. The Secretary did not write such an EIS. Meanwhile ADF&G implemented the program, making up to 30 permits for pilot–gunner teams available for issuance in November, a period of short days and poor snow cover. Few teams participated because most were waiting for the more favourable day length and snow conditions of late February. In February, however, court action ensued as follows:

4 Feb. 1977. Defenders of Wildlife *et al.*[1] filed suit against the Secretary of the Interior in US District Court for DC. The plaintiffs contended that two federal statutes, the Federal Land Policy and Management Act of 1976 (FLPMA) and the Alaska Native Claims Settlement Act required that the Secretary provide an EIS; they asked for an injunction.

14 Feb. 1977. The judge for the DC District court issued a preliminary injunction compelling the Secretary to order the State to halt the program on BLM-administered lands in GMUs 23, 24, and 26 (see Secretarial Order No. 2999 of 17 February 1977).

22 Feb. 1977. The State of Alaska and the Mauneluk Association, an Alaskan native organization, filed suit in US District Court for Alaska against the Secretary of the Interior (defendant) and Defenders of Wildlife *et al.* (intervenors) asking for a stay of the DC court's order. The State asked the court to declare that the Secretary had no power to stop the control effort.

1 Mar. 1977 (approx. date). The Secretary of the Interior appealed the injunction to the Court of Appeals for DC.

16 Mar. 1977. The judge in Alaska District

[1]Natural Resources Defense Council; Int. Fund for Animal Welfare — US; The Humane Society of the US; the Fund for Animals; Animal Welfare Institute; The Wild Canid Survival and Research Center — Wolf Sanctuary; Friends of the Earth, Inc.; and 7 private parties.

Court declared in a preliminary finding that Alaska should have been a party to the case. He declared that no EIS was required. However, he did not grant the request for a stay of the DC Court's injunction, contending that two opposing decisions of District Courts placed the Secretary of the Interior in an untenable position.
11 Apr. 1977. The judge in the Alaska District Court case reaffirmed his preliminary finding. He also held that the Secretary of the Interior had the power to halt the wolf control program, but that an EIS was not required because the Secretary refrained from exercising that power.
21 July 1977. The State of Alaska appealed the judge's decision in the Alaska District Court case to the US Court of Appeals, Ninth Circuit. The State contended that the Secretary did not have power to halt programs. Eleven other states and the International Association of Fish and Wildlife Agencies joined as interested parties; the issue was rapidly widening to cover all non-migratory wildlife.
26 July 1977. Defenders of Wildlife *et al.* appealed the Alaska District Court judge's decision on EIS. They asked for confirmation of the judge's ruling on the authority of the Secretary to stop the control hunts.
22 Feb. 1979. The Ninth Circuit Court ruled that the Secretary of the Interior was not required to file an EIS, but it did not rule with regard to the power of the Secretary.
16 Mar. 1979. Court of Appeals for DC rescinded the injunction on Western Arctic Caribou Herd "for want of equity", and directed that the complaint be dismissed. "In an unpublished memorandum accompanying our order, we said that '[s]ound principles of comity dictate that this court should not undertake an independent examination of issues resolved by the Ninth Circuit ruling' ".
28 Feb. 1980. The Secretary of the Interior filed Secretarial Order No. 3047 in the Federal Register rescinding the previous order closing all BLM-administered lands in GMUs 23, 24, and 26 to aerial hunting.

The court cases during 1977 again centred on NEPA requirements. The cases raised and clarified several important issues regarding EISs but failed to address one concerned with federal–state authority.

The Ninth Circuit Court, ruling on an appeal from the Alaska District Court decision, avoided the issue of federal–state authority, but did specify that the non-exercise of any authorities and duties possessed by the Secretary does not require an EIS. Also, the Ninth Circuit judges were reluctant to impose NEPA requirements in the absence of federal funding, as occurred in the Western Arctic herd action.

The Court of Appeals for DC essentially affirmed the Ninth Circuit Court's decision and reversed the injunction issued by the District Court for DC.

Although court action stymied western arctic wolf control after only nine wolves had been taken, the caribou herd was probably exposed to decreased wolf predation during the winter. Unexpectedly, about half the herd stayed throughout the winter on their summering area north of the Brooks Range; that area has low wolf densities (ADF&G 1977, unpubl. rep.). Of the half that wintered south of the Brooks Range, 75% wintered in an area from which 75 wolves were removed by the short-lived control action and by intensive private trapping and hunting. The latter was probably by Alaskans disgruntled over the litigation that stopped the control effort. In all of GMUs 23 and 24, nearly 200 wolves were taken by trappers and hunters during the winter of 1976/77 (ADF&G 1977, unpubl. rep.).

The wolf-reduction program in GMU 20A continued during the winter of 1976/77, with 27 wolves taken by the ADF&G control program and 26 more by trappers and hunters (ADF&G 1979, unpubl. issue paper 79-07). By April 1977 the wolf/moose ratio was estimated to be 1:50–80 (ADF&G 1977, unpubl. rep.). The decline in the moose herd was arrested and there was substantially increased survival of calves and yearlings in the control area. In adjoining areas with no reductions in wolves, the calf and yearling survival rates appeared unchanged from the pre-control levels (Hinman 1978, ADF&G Fed. Aid Wildl. Rep.).

The GMU 13 control study continued. During the winter of 1976/77, 12 wolves that either moved into the experimental area or had been there since the inception of the study were removed, bringing the total removed to 52 (ADF&G 1979, unpubl. issue paper 79-07). Moose-calf survival appeared to be slightly better in the wolf reduction area than outside it, based on mortality of radio-collared moose calves, but brown bear predation appeared to be a significant mortality factor (Ballard *et al.* 1981). ADF&G initiated a study to measure this.

No new wolf control programs were started during the winter of 1977/78. The program continued in GMU 20A with 39 wolves taken by ADF&G and 4 by trappers, resulting in a fall wolf/moose ratio of 1:40 by 1978. The moose population continued to increase; the available data suggested a 15% annual increase in the control area and only a 1% increase outside it. The pre-control population of 2900 moose in the fall of 1975, with a ratio of 14 calves/100 cows, reached 3500 by the fall of 1978, with a ratio of 50 calves/100 cows (ADF&G 1979, unpubl. issue paper 79-07). The results convinced ADF&G and the Board of Game that the control action in GMU 20A was the primary factor responsible for the increases. Furthermore, a wolf/moose ratio of 1:50, and not the originally proposed 1:100, seemed adequate for desirable growth.

The GMU 13 control study continued in 1977/78. Seven wolves were taken in the experimental area (ADF&G 1979, unpubl. issue paper 79-07). The moose–bear study confirmed that bears were causing heavy mortality to calves for several weeks after birth, creating additional problems for managers responsible for moose management (Ballard *et al.* 1981).

The success in GMU 20A stimulated an increased demand by residents elsewhere for wolf control in their areas. Recognizing that additional wolf control projects were likely, the Board took steps during the spring of 1978 to make wolf control a routine management task for ADF&G and not a special action imposed by the Board. On 7 April 1978 the Board adopted a Statement of Direction indicating the Commissioner could permit the use of aircraft in wolf control when he found that all the following conditions prevail:

1) the highest priority use of wildlife in an area is determined to be the use of prey species for food or recreational hunting;

2) the prey populations have been reduced to or are held at a level below that deemed to be the capacity of the habitat;

3) the prey populations are below levels that could reasonably satisfy the priority uses;

4) adequate control of predation cannot be accomplished by manipulation of hunting and trapping seasons and bag limits;

5) predation control based on aircraft use governed by a permit is judged to be an effective method for that area, and;

6) such predation control in an area can be adequately supervised and regulated.

The Commissioner was no longer always expected to seek prior approval before implementing aerial hunting, but he was directed to keep the Board informed of his actions.

An ADF&G report presented to the Board on 28 November 1978 identified seven new areas with chronically low ungulate populations that were being considered for wolf reductions. The ADF&G staff prepared issue papers for these areas and submitted them to the Commissioner for his approval.

By December 1978, Alaska lands legislation, which would ultimately be enacted and entitled the Alaska National Interests Lands and Conservation Act, was a sensitive issue in Washington, DC, and in Alaska. The entire series of legislative proposals was commonly referred to as "d(2)" legislation. Any Alaskan issue that could be controversial, both within and outside Alaska, received intense scrutiny with respect to repercussions on d(2). Consequently, the political ramifications as well as the biological worth of the new wolf-control projects needed careful evaluation. Four of the projects were deleted by the Commissioner before he informed the Governor of the proposed actions.

ADF&G held seven public meetings to assess reaction to the three remaining proposals; the reaction was mostly favourable. However, the Commissioner, caught between concerns of national and local politics, sought concurrence from the Board before acting. Meanwhile the GMU 20A control continued (18 wolves were removed during the winter), as did the GMU 13 control study in which 2 wolves were removed (ADF&G 1979, unpubl. issue paper 79-07).

The Board agreed on 9 March 1979 to wolf control in three new areas: GMUs 19A and B; the Innoko drainage of GMU 21; and the Nowitna drainage of GMU 21. The stressed populations were moose. All but GMU 19B are areas of importance to local subsistence hunters. Wolf/moose ratios in GMUs 19A and B, the Innoko, and the Nowitna were estimated (later revised) to be 1:15, 1:28, and 1:10 respectively. Issuing of aerial hunting permits to private pilot–gunner teams commenced on 11 March 1979.

The three new actions immediately provoked controversy. The Special Committee on Subsistence in the Alaska Legislature, in a news release dated 22 February 1979, criticized the actions as politically unwise in regard to d(2). Two court cases were initiated as follows:

12 Mar. 1979. Defenders of Wildlife *et al.*[1] filed suit against the Secretary of the Interior *et al.* in US District Court for DC, asking for declaratory and injunctive relief. The plaintiffs contended that the secretary had authority over control programs based on the Federal Land Policy and Management Act (FLPMA); hence an EIS was required.

13 Mar. 1979. The District Court for DC issued a temporary restraining order that enjoined the Secretary to "... take all steps necessary to halt aerial killing of wolves by agents of State of Alaska. . . ." on the federal lands in the three control areas.

23 Mar. 1979. The District Court for DC issued a preliminary injunction and ruled that an EIS was needed. The Court also denied the Secretary's requests that the case be transferred to the US District Court for Alaska and that the action be dismissed for failure to join Alaska as an indispensable party.

Mar. 1979. Three private parties filed a case against ADF&G *et al.* in Alaska Superior Court, Third Judicial District, contending that the Board of Game had delegated powers to the Commissioner in excess of those authorized by the Legislature, and that the Governor had exerted undue political influence regarding the proposed wolf control projects. A requested temporary restraining order was denied.

Early Apr. 1979. The Secretary of the Interior *et al.* appealed the District court ruling to US Court of Appeals for DC.

31 Mar. 1979. The Secretary of the Interior filed Secretarial Order No. 3036 in the Federal Register, which closed all BLM-administered lands in the three control areas (GMUs 19A, 19B, and 21) to aerial hunting.

Aug. 1979. The Superior Court judge dismissed the case, ruling that proper authority existed and that no undue political influence was evident.

5 Feb. 1980. The Court of Appeals for DC ruled that the Secretary was not required to file an EIS. It also ruled on the authority of the State in wolf control (see below).

28 Feb. 1980. The Secretary of the Interior filed Secretarial Order No. 3047 in the Federal Register, which rescinded previous order (No. 3036).

The Alaskan Superior Court case emphasized the political sensitivity in Alaska. In a memorandum supporting a motion for summary judgement filed with the Court on 2 April 1979, the attorney for the plaintiffs stated:

> This hunt, willingly or not, is a factor in the Congressional dynamics surrounding the d(2) deliberations. It has raised questions regarding the State's ability to manage wildlife (both moose and wolves), created controversy among the constituents of Congressmen from urban areas far removed from Alaska, and created some controversy between subsistence hunters and environmentalists who support a strong d(2) bill. Whether one views this hunt as a gesture of political suicide, or as a carefully orchestrated, if unsuccessful, attempt to split the ranks of the backers of the bill, it is clear that the hunt is enmeshed in political controversy.

[1]Natural Resources Defense Council, Inc.; Int. Fund for Animal Welfare; The Humane Society of the United States; the Fund for Animals; Animal Welfare Institute; The Wild Canid Survival and Research Center — Wolf Sanctuary; World Wildlife Fund — US; and 2 private parties.

The actions in the DC courts essentially reaffirmed previous court findings regarding EISs. In addition, an important statement on state–federal authority emanated from that action.

The Defenders of Wildlife *et al.*, in their suit in District Court for DC, contended that FLPMA gave the Secretary of the Interior the power to close federal lands to the wolf control program, hence an EIS was needed regardless of whether he exercised those powers. The Court of Appeals for DC spoke directly to the authority question, stating that under the BLM Organic Act, Congress "... assigned the states the primary responsibility for the management of wildlife programs within their boundaries". The Court did note that Congress may pre-empt state management of wildlife on federal lands, but there must be clear intent by Congress to do so. In summary the Court stated, "Far from attempting to alter the traditional division of authority over wildlife management, FLPMA broadly and explicitly reaffirms it". The Circuit Court of Appeals reversed the District Court's ruling.

The hunts during the spring of 1979 accounted for 29, 11, and 5 wolves in GMUs 19A and B, the Innoko, and the Nowitna respectively. ADF&G judged the hunts effective only in the Aniak River drainage in GMU 19A; bad weather and closure of federal lands substantially decreased effectiveness in the other areas (ADF&G 1979, unpubl. issue paper 79-07).

During the fall of 1979, ADF&G presented to the Board issue paper 79-07 and supporting material about wolf control programs. The paper contained a statement clarifying the agency's position on wolf control, as follows:

> The Department of Fish and Game acknowledges, as a basic proposition, that wolf-reduction programs which are intended to rehabilitate depressed ungulate populations are not needed to increase the population of either predator or prey species, but are for the sole purpose of providing more animals for human consumption.

The issue paper also reaffirmed that ADF&G would reduce wolf numbers only in response to a specific problem in a specific area; the Department would not issue aerial permits for sport-hunting purposes.

The issue paper made three recommendations for the winter and spring of 1980: first, that the control operations previously initiated in GMUs 19A, 19B and 20A be continued; second, that the programs in the Innoko and Nowitna drainages of GMU 21 be cancelled "due to budgetary constraints and in recognition of marginal effectiveness of wolf reductions in these areas as long as federal lands remain closed" (although a subsequent decision continued the operations in both areas); and third, that control be initiated in three new areas in GMU 20. Two of the new areas had depressed moose populations showing virtually no improvement even with very restrictive hunting seasons and bag limits (ADF&G 1979, unpubl. rep. issue paper 79-07). The other area had reduced moose and caribou populations.

Private pilot–gunner teams, under limited permits, were to conduct the operations, with the number of wolves to be removed from each unit specified. Based on the experience in GMU 20A, ADF&G managers hoped to establish a wolf/moose ratio of 1:50, rather than the previously used 1:100 ratio.

A fourth new area that had previously been included for control was deleted; the reason was given as follows:

> In spite of the fact that all biological data strongly support the need for temporary wolf reduction in the area, the Department believes that it would not be in the best interests of the State to attempt a reduction program at this time. Factors involved in this decision include the proposed Yukon-Charlie federal withdrawal, the large percentage of other federal land, and the sensitivity of the land settlement question.

The control operations in GMUs 23 and 24 (the Western Arctic Caribou Herd action), begun in 1977, were still halted by a Secretary of the Interior's order, as mentioned earlier. The order was only lifted on 28 February 1980, after the Court of Appeals in DC ruled favourably for the State.

The new wolf control operations did not occasion substantial new controversy, although several organizations such as Greenpeace did voice opposition. Apparently the public, particularly in Alaska, was accepting ADF&G's and the Board's assertions that, in order to attain goals they had defined following public input, both prey and wolves must be managed. Operationally, wolf control was becoming more of a routine management activity and less of a special, high visibility event requiring extensive public hearing and debate.

The wolf control situation during the winter of 1980/81 essentially remained unchanged from that of 1979/80. Even though all legal prohibitions against control were lifted with the 5 February 1980 Appeals Court decision, control operations were not resumed in the winter range of the Western Arctic herd. That herd had increased substantially, due to favourable winters, to restrictive hunting seasons and bag limits, and to the fact that most of the herd continued to winter in areas of low wolf densities.

The wolf control program in GMU 20A, initiated in the spring of 1976, is considered a success by ADF&G and the Board. Although the desired level of wolf reduction was never achieved, a dramatic increase in moose numbers occurred in the control area. The interim management objective of 5000 moose will be reached within 2 or 3 years. Whether that stocking level is the desired one in terms of habitat conditions, wolves, and humans is still an open question. Based on the desires of the public, particularly those living near the area, the main use of GMU 20A's wildlife resources is the consumptive use of moose. In order to sustain this use, it may be necessary to maintain wolf populations at an artificially reduced level.

What of the future?

Alaska's growing human population coupled with increased use of land for agriculture, forestry, mineral production, and urbanization will steadily reduce the habitat available for wildlife, especially the many wide-ranging mammals. The Alaska National Interests Lands and Conservation Act has resulted in park or monument status, and thus legal protection for wolves, for about 6% of the gross area of the State. Seven of the National Park Service areas under complete legal protection each exceed 6900 km^2, and most units in this group exceed 13 000 km^2. These areas are well distributed over the entire State except in the southeast panhandle. In addition, this legislation placed another 5% in "preserve" status; although hunting will be permitted on preserves, wolf control is unlikely. The new refuges and the Forest Service's National Monuments in southeast Alaska probably have a similar status. It will be difficult to define or map the status of wolves on specific lands until regulations provided for under the d(2) legislation have been promulgated.

The demands on wildlife populations will increase significantly as the rural human population continues to grow, as the road system expands, and as the nation's food supplies become more expensive or scarcer for reasons paralleling the above. Consumption of wildlife will continue to be assigned high priority in Alaska on lands not managed intensively for primary uses incompatible with wildlife production. There will certainly be strong pressure for the control of wolf populations in areas from which humans are attempting to gain the highest possible yield of wild meat.

We anticipate further acceptance among ecologists and eventually the public of the role of predators in depressing prey populations and in prolonging recovery from lows caused by predation and other factors. The effectiveness of bears as predators in certain situations will be better understood; however, it seems that adjustments of hunting pressure on bears can substitute for "control" in this case. Wolf control will continue to become more of an operational process for ADF&G but will be conducted within clearly stated goals and criteria. The agency, working with the public, is well along in the development of detailed population-level management plans. Additional study is needed to understand sufficiently both predator–prey interactions and the most effective strategies of control.

Although it may appear to some that wolf management in Alaska has come full circle, the second round will be made under vastly different conditions and much stricter rules. ADF&G policy will probably continue to preclude poisons except in the most extreme circumstances; aerial hunting, objected to by some as unfair, is one of the most target-specific control methods possible; and wolf reduction will be directed at clearly specified areas. We hope that the future will be characterized by substantially increased knowledge of basic ecology and significantly more effective and mutually sympathetic communication between the many interested segments of society.

Biology and management

(photo: Tom Hall)

Population dynamics of wolves

Lloyd B. Keith

1. Abstract

This paper first examines rates of increase among wolf populations in North America. These rates, together with recruitment indices (% pups) and reported numerical trends, are then collated with wolf and ungulate densities and with rates of human exploitation. The analysis indicates that rates of increase are primarily determined by the per-capita biomass of their ungulate food supply, and that wolf densities in stationary populations are thereby adjusted to total ungulate biomass. Human exploitation of wolf populations probably affects rates of increase by reducing densities and thus elevating per-capita food resources. Compensatory increases in reproduction or pup survival permit an estimated sustained harvest of about 30% of fall populations. The functional- and numerical-response characteristics of wolves suggest potentially strong density-dependent predation on ungulates, but with lags that would induce recurrent fluctuations.

2. Introduction

Field research that began in the late 1950s produced the first real quantification of wolf (*Canis lupus*) population demography and dynamics (Mech 1966, Rausch 1967, Pimlott *et al.* 1969). Thereafter, information accumulated rapidly, and today we probably know more about wolves than about any other mammalian predator. In some respects, however, the synthesis and evaluation of data, particularly those pertaining to demographic information, are not up to date, and this paper attempts to remedy the situation.

Studies of population dynamics seek basically to understand how rates of increase are determined, and thus how numbers are controlled over time. Accordingly, this paper examines rates of increase and population trends among wolves, and collates these parameters with wolf densities, food resources, and human exploitation. Some management implications of the analysis are then discussed.

3. Definitions and data sources

The term "rate of increase" refers here to the rate at which the *number* of individuals in a population changes annually; it does not refer to, nor have I estimated it from, the percentage of young or yearlings in the population at some designated time. Both finite (λ) and exponential (r) rates of increase are given, the former being the coefficient of growth annually (in a population that doubles, $\lambda = 2$), the latter being its natural logarithm ($r = \ln \lambda$). Notations of exponential rate of increase ($\bar{r}$, r_s, r_m and r_p) and definitions follow Caughley (1977, p.109). I calculated mean rates of increase from annual population estimates (N_t) by regressing $\ln N_t$ against time in years (t); the slope of the regression line was then $\bar{r}$, and its antilog was $\bar{\lambda}$.

In reviewing the literature I tried to distinguish between information having some quantitative basis and that originating from subjective appraisals and intuition. There was often a fine line here, however, and I could certainly have erred. Several early estimates of wolf density by Clarke (1940), Murie (1944), Cowan (1947), and Rowan (1950), for example, were excluded from the analysis, but may well have been as accurate as other later estimates based on aerial observations or harvests.

The reader may notice that I have not used wolf population estimates given by Rausch (1969) for south-central Alaska to calculate a rate of increase. These estimates were questioned and revised greatly by Van Ballenberghe (1981), who stated that Rausch's figures were probably "conservative approximations of actual population size". He concluded also that illegal hunting had impeded recovery of this allegedly protected wolf population. Furthermore, one cannot now be sure what year population growth ceased.

I have drawn freely on unpublished data from many workers, and am grateful to them for permission to do so. The data sources are

Table 1
Rates of increase observed in wolf populations

Location and size of study area	No. of years of increase	Mean annual rates of increase calculated from successive population estimates: Exponential (r)	Finite (λ)	Data sources*
Alberta (Peace River District)	2 (1976–78)	0.380	1.46	(1)
Michigan (Isle Royale: 544 km²)	7 (1952–59)	0.326	1.39	(2)
Alaska (Anaktuvak Pass: 9300 km²)	2 (1971–73)	0.290	1.34	(3)
Minnesota (Beltrami Island State Forest: 2700 km²)	2 (1974–76)	0.272	1.31	(4)
Alberta (Fort McMurray: 2800 km²)	2 (1975–77)	0.191	1.21	(5)
Ontario (Algonquin Park: 1700 km²)	6 (1965–71)	0.182	1.20	(6)
Michigan (Isle Royale: 544 km²)	7 (1969–76)	0.144	1.15	(7)
Means		0.255	1.29	

*(1) Bjorge R.R. 1979, Alberta Fish and Wildl. Div., unpubl. rep.
(2) Mech 1970.
(3) Stephenson and Sexton 1974, Wolf rep., Alaska Fed. Aid Wildl. Rest. Prog. Rep. Project W-17-8.
(4) Fritts and Mech 1981.
(5) Fuller and Keith 1980.
(6) Theberge and Strickland 1978: probably a minimum estimate because it presumes that pack size did not change with population increase.
(7) Peterson 1977.

Moose are major prey of wolves in boreal forests (photo: R. Boonstra)

Table 2
Rates of increase and percentage of pups in age-stable populations generated from reported age-specific rates of survival and reproduction of wolves

	Annual survival rates			Annual reproduction			Calculated age ratios and survival-fecundity rates of increase after attainment of stable age distribution		
					Litter size				
Population*	First-year (pup)	Second-year (yearling)	Later-year (adult)	Yearlings and adults pregnant (%)	Yearling	Adult	Pups in mid-winter (%)	Exponential rate of increase (r_s) annually	Finite rate of increase (λ_s) annually
A	0.48	0.63	0.78	90	5.4	6.5	55	0.282	1.33
B	0.34	0.63	0.78	90	5.4	6.5	50	0.223	1.25
C	0.34	0.63	0.78	60	5.0	5.0	38	0.071	1.07
D	0.34	0.65	0.65	60	5.0	5.0	39	0.007	1.00

*Population A combines the high survival of pups in exploited populations with the high survival of yearlings and adults in unexploited populations; survival calculated from Mech (1970, Table 6). Reproductive data are from exploited populations in Alaska (Rausch 1967). Resulting rates of increase probably approach the maximum attainable by wolves in the wild under favourable conditions.
Population B combines the lower survival of pups in unexploited populations (Mech 1970, Table 6) with the same yearling and adult survival and reproduction as for population A.
Population C combines the lower reproduction of unexploited populations in Ontario (Pimlott *et al.* 1969) with survival rates for unexploited populations utilized for population B.
Population D combines survival rates of yearlings and adults, as measured by radio-telemetry in an unexploited population in Minnesota (Mech 1977*a*, Table 9), with pup survival and reproductive in an unexploited population in Ontario (Mech 1970, Table 6; Pimlott *et al.* 1969). The annual yearling-and-adult survival rate of 0.65 is the mean for the 3 years (1970, 1973, 1974) when the population was most stationary.

fully acknowledged, but I am solely responsible for any errors in interpretation that may have occurred.

4. Rates of increase

Mean exponential rates of increase observed in seven wolf populations ranged from 0.144 to 0.380 annually, averaging 0.255 overall (Table 1). Three of these populations were being hunted or trapped, but their rates of increase were comparable to the four that were unexploited. The rate of increase observed on Isle Royale during 1952–59 ($\bar{r}$ = 0.326, $\bar{\lambda}$ = 1.39) probably approaches the maximum or intrinsic rate (r_m) for wolves, as this population was initiated by a few individuals with abundant food.

A second estimate of r_m was obtained by calculating a survival-fecundity rate of increase (r_s) from the highest reproductive and survival rates reported among wolves in the wild. The resulting estimate of r_m was 0.282 (Table 2, line 1). Because both the accuracy and precision of data used in these estimations of maximum rate of increase are not assessable, their mean of 0.304 is likely to be our best estimate of r_m (λ_m = 1.36) for wolf populations in the wild. This compared with a theoretical exponential rate of 0.833 (λ = 2.30) given maximum reproduction (Rausch 1967), a stable age distribution and no deaths. Obviously, survival rates are greatly depressed even in the most favourable environments.

5. Effects of food resources and wolf densities on rates of increase

The overwhelming dependency of wolf populations on one or more ungulate species in winter, and continued high dependency in summer, is well documented (Pimlott 1967*b*, Mech 1970, Peterson 1977, Fuller and Keith 1980, and many others). To test whether such dependency was reflected in observed rates of increase (Table 1), the latter were compared with existing ungulate populations. Because three ungulate species of marked different size were in-

Table 3
Observed rates of increase in wolf populations vs. wolf and ungulate densities

Location	Ungulate densities in winter* Mean no. per 100 km²	Mean biomass index†	Wolf densities in winter* Mean no. per 1000 km²	Ungulates per wolf in winter* Mean no.	Mean biomass index†	Mean annual finite rate of increase($\bar{\lambda}$) in wolf population‡	Ungulate data sources§
Alberta (Peace River District)	130 moose	780	11.0	118 moose	708	1.46	(1)
Michigan (Isle Royale)	147 moose	882	19.9	74 moose	444	1.39	(2)
Alaska (Anaktuvak Pass)	72 moose	432	6.0	120 moose	720	1.34	(3)
Minnesota (Beltrami Island State Forest)	500 deer 30 moose	680	16.8	298 deer 18 moose	406	1.31	(4)
Alberta (Fort McMurray)	18 moose	108	5.5	33 moose	198	1.21	(5)
Ontario (Algonquin Park)	300 deer 17 moose	432	24.2	136 deer 7 moose	178	1.20	(6)
Michigan (Isle Royale)	162 moose	972	50.2	32 moose	192	1.15	(7)

*Based on the average of numbers present annually during years of wolf population increase.
†Moose, caribou, and deer were assigned relative biomass values of 6, 2, and 1, respectively, based on mean weights of adults in winter.
‡See Table 1 for wolf data sources and years of population increase.
§(1) Bjorge, R.R. 1979, Alberta Fish and Wildlife Div., unpubl. rep.
(2) Krefting 1951, Mech 1966, Peterson 1977.
(3) Stephenson and Sexton 1974, Wolf rep., Alaska Fed. Aid Wildl. Rest. Prog. Rep. Project W-17-8.
(4) Fritts and Mech 1981.
(5) Fuller and Keith 1980.
(6) Pimlott *et al.* 1969, Theberge and Strickland 1978.
(7) Peterson 1977.

volved, ungulate density was first converted to relative biomass by multiplying numbers per 100 km² by coefficients of 6, 2, and 1 for moose (*Alces alces*), caribou (*Rangifer tarandus*), and deer (*Odocoileus virginianus*), respectively. Observed rates of increase were unrelated to this ungulate biomass index (Table 3, columns 3 and 7).

Social interactions among wolves, intensifying with density, have been alleged to reduce or prevent population growth (Murie 1944, Pimlott *et al.* 1969, Mech 1970, Peterson 1977, Carbyn 1981). Rates of increase were, on the whole, poorly correlated with density, but they were lowest in the two highest-density populations (Table 3, columns 4 and 7). Furthermore, the much lower rate of increase on Isle Royale during the second period of wolf population growth (1969–76) occurred at densities averaging 2.5 times those of the first period (1952–59); moose numbers were similar in each period.

I next explored possible joint effects of ungulate and wolf densities. Comparison of rates of increase with ungulate biomass *per wolf* (Fig. 1) yielded a highly significant correlation ($r = 0.87$, $P = 0.01$).

If, as this suggests, ungulate biomass and wolf density interact to influence rates of increase, then one might also expect a correlation between ungulate biomass per wolf and indices of recruitment [or of potential rate of increase (r_p)] within wolf populations generally. Field studies have indicated that a good index of annual recruitment is percentage of pups in fall or winter (Peterson 1977, Fritts and Mech 1981), and this is supported by the calculated percentage of pups in four age-stable wolf populations with finite rates of increase between 1.00 and 1.33 (Table 3). The percentage of pups reflects both reproduction and pup survival through summer relative to that of adults.

There were eight exploited wolf populations for which I could calculate ungulate/wolf ratios and percentage of pups (Table 4). These populations had a 50-fold range in density, and their ungulate prey an 8-fold range in biomass. Some of the wolf populations were stationary, others were either increasing or decreasing. The correlation between percentage of pups and ungulate biomass per wolf (Fig. 2)

Table 4
Relationship of wolf population parameters to relative abundance of ungulates in exploited populations

Location	No. of winters	Ungulates per wolf in winter: No. of ungulates	Ungulates per wolf in winter: Biomass index*	Fall or winter wolf populations: Pups (%)	Fall or winter wolf populations: Existing population trend	Fall or winter wolf populations: Density (/1000 km²)	Data sources†
Alaska (Interior: GMU 20A)	1 (1975–76)	16 moose	96	30	Stationary	13.2	(1)
Ontario (Algonquin Park)	2 (1957–59)	150 deer 4 moose	174	35	Stationary	38.5	(2)
Minnesota (Northeastern)	3 (1969–72)	122 deer 17 moose	224	40	Stationary	41.7	(3)
Alaska (South-central: GMU 13)	1 (1975–76)	47 moose 23 caribou	328	43	Stationary	6.5	(4)
Alberta (Peace River District)	1(1977–78)	88 moose	528	43	Increasing	14.7	(5)
North-central Canada (Barren-ground caribou range)	1(1957–58)	151 caribou	302	46	Declining	1.7	(6)
Alaska (Anaktuvak Pass)	2 (1971–73)	121 moose	726	64	Increasing	6.0	(7)
North-central Canada (Barren-ground caribou range)	1 (1960–61)	306 caribou	612	73	Declining	0.8	(6)

*Moose, caribou, and deer were assigned relative biomass values of 6, 2, and 1, respectively, based on mean weights of adults in winter. Ungulate biomass values are the products of relative biomass values times ungulate numbers per wolf.

†(1) Stephenson 1978, Alaska Fed. Aid Wildl. Rest. Prog. Rep. Project W-17-3. Haggstrom and Buchholtz 1978, Alaska Fed. Aid Rest. Prog. Rep. Project W-17-9.
(2) Pimlott *et al.* 1969.
(3) Van Ballenberghe *et al.* 1975. Mech and Karns 1977.
(4) Stephenson and Van Ballenberghe 1978, Alaska Fed. Aid Wildl. Res. Prog. Rep. Project W-17-8; moose density estimated from ratio of bull kill (1965–71/1972–76)(Eide 1980, Alaska Fed. Aid Wildl. Rest. Prog. Rep. Project W-17-11), and estimated density of one moose/1.88 km^2 in 1965 (Rausch 1969); caribou density taken as mean for years 1972, 1973, and 1976 (Eide 1978, Alaska Fed. Aid Wildl. Rest. Prog. Rep. Project W-17-9).
(5) Bjorge, R.R.; Myers, J.; Gunson, J.R. 1979, Alberta Fish and Wildl. Div., unpubl. rep.
(6) Kelsall 1968; for wolf density calculations see footnote (8), Table 7; caribou densities from Parker (1971).
(7) Stephenson and Sexton 1974, Alaska Fed. Aid. Wildl. Rest. Prog. Rep. Project W-17-8.

Figure 1
Relationship of annual finite rates of increase of seven wolf populations to the per-capita biomass of ungulates present (data from Table 3)

Figure 2
Relationship of percentage of pups in eight exploited wolf populations during fall or winter to the per-capita biomass of ungulates present (data from Table 4)

Figure 1

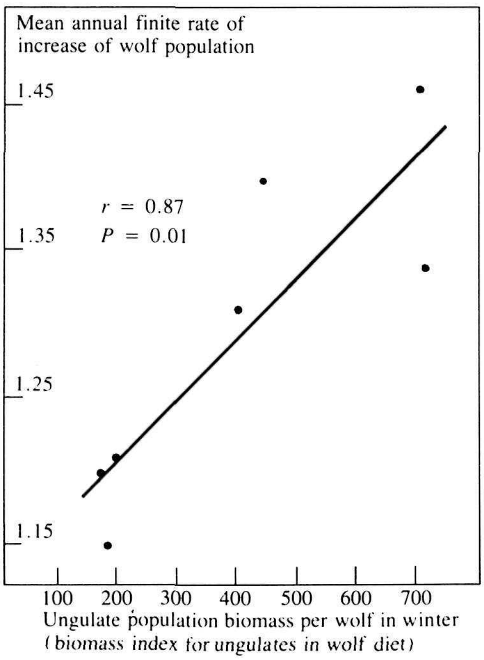


Figure 2

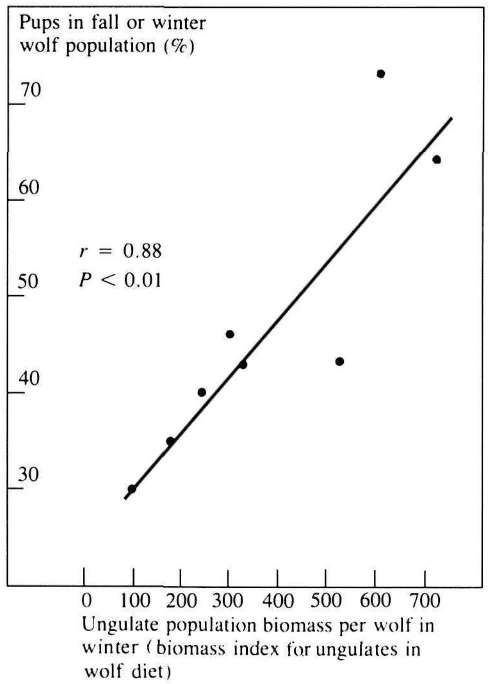


Table 5
Percentage of pups in unexploited wolf populations during fall and winter

Location	No. of winters	Pups in fall or winter population (sample size) (%)	Existing population trend	Data sources*
North-central Canada (Northeast of Great Slave Lake)	1 (1955–56)	13 (136–381)	Stationary	(1)
(Wood Buffalo National Park)	1 (1951–52)	19 (58)	Stationary	(2)
Ontario (Algonquin Park)	2 (1964–66)	31 (106)	Stationary	(3)

*(1) Kelsall 1968.
(2) Fuller and Novakowski 1955.
(3) Pimlott *et al.* 1969.

was highly significant ($r = 0.88$, $P<0.01$), and thus provided further evidence of a joint impact of food and density on rates of increase.

6. Effects of human exploitation on age distribution and population trend

The idea that high-density unexploited wolf populations have lower pup/adult ratios than low-density exploited populations was apparently first expressed by Fuller (CWS 1954, unpubl. rep.). Pimlott *et al.* (1969) summarized age-ratio data available for 1967 and concluded that:

> Percentages [of pups] of 15 to 30 are indicative of saturated, stable populations; 40 to 50 indicate populations that are being moderately to heavily exploited.

Mech (1970, pp. 59–62) likewise pointed to the evident increase in percentage of pups in exploited populations, but did not attempt to associate this increase with high density or saturation.

To my knowledge, the percentage of pups in unexploited stationary populations has been recorded on just three occasions (Table 5). In two cases pups comprised less than 20%, well below the 30–73% recorded in exploited populations (Table 6). The third unexploited population had 31% pups. Densities ranged widely from about 1 wolf/375 km^2 (13% pups) to 1/26 km^2 (31% pups).

The strong correlation between per-capita food supply and percentage of pups in exploited populations (Fig. 2) prompted a similar examination of the two unexploited populations for which food supplies could be estimated. Transition of the stationary Algonquin Park wolf population from exploited to unexploited status was evidently accompanied by little if any change in the relatively low ungulate biomass index of 174 per wolf; nor was there a significant change in the percentage of pups (35% as against 31%). The unexploited population near Great Slave Lake which contained only 13% pups also had a low per-capita ungulate biomass index (188).

Van Ballenberghe *et al.* (1975) concluded that survival of pups from birth to 7 months was similar in one unexploited and two exploited populations. They suggested that higher birth rates were the main demographic reason for the greater percentage of pups in exploited populations, but did not speculate on why this came about. One explanation is that exploitation disrupts the social organization within packs, thereby affecting social behaviour that would otherwise limit recruitment. Alternatively, exploitation may simply lower wolf densities, thereby increasing per-capita food supplies. In either case, both birth rate and pup survival could be affected. Another view (R.O. Peterson, pers. comm.) is that exploitation reduces pack size, and thereby increases the percentage of pups because each pack has only one litter and litter size *per se* does not change. Peterson further proposed that wolf population densities are then maintained through establishment of additional small packs. Peterson's model of wolf response to exploitation thus incorporates elements of changing social structure (smaller packs lead to fewer non-breeding females) and adjustment to food supply (smaller packs mean more packs).

Comparison of reported exploitation rates with resulting numerical trends in 13 wolf populations (Table 7) suggests that declines occurred when overwinter harvests exceeded about 38% of fall densities. Compensatory increases in reproduction and/or survival can apparently offset lower rates of exploitation. Although the percentage of pups in exploited populations is directly related to food supplies (Fig. 2), it gives little indication of population trend (Tables 4 and 6). There is a tendency for exploited stationary populations to have fewer pups (30–43%), but pups may comprise 43–73% of other populations that are either increasing or decreasing with exploitation. This is perhaps further evidence of per-capita food supplies governing recruitment and thus percentage of pups because, first, wolf populations increasing under exploitation are clearly below densities at which food shortage limits recruitment, whereas stationary exploited populations may not be. Second, populations declining under exploitation have, as a consequence, increased per-capita food supplies but their exploitation rates are too high to be fully compensated. This interpretation is consistent with available information on percentage of pups, population trends, and per-capita food supplies (Tables 4 and 6).

Table 6
Percentage of pups in exploited wolf populations during fall and winter

Location	No. of winters	Pups in fall or winter population (sample size) (%)	Existing population trend	Data sources*
Alaska (Interior: GMU 20A)	1 (1975–76)	30 (131)	Stationary	(1)
Ontario (Algonquin Park)	2 (1957–59)	35 (48)	Stationary	(2)
Minnesota (Northeastern)	3 (1969–72)	40 (121)	Stationary	(3)
Alaska (South-central: GMU 13)	1 (1975–76)	43 (77)	Stationary	(4)
Alberta (Peace River District)	1 (1977–78)	43 (54)	Increasing	(5)
Alaska				
(Interior)	7 (1959–66)	43 (2541)	Increasing	(6)
(South-central: GMU 11, 12, and 13)	1 (1967–68)	45 (60)	Declining	(7)
North-central Canada (Northeast of Great Slave Lake)	1 (1957–58)	46 (381)	Declining	(8)
Alaska				
(Arctic)	7 (1959–66)	48 (1196)	Declining or stationary	(6)
(South-central)	2 (1964–66)	60 (251)	Increasing	(6,7)
(Anaktuvak Pass)	2 (1971–73)	64 (84)	Increasing	(9)
North-central Canada (Northeast of Great Slave Lake)	1 (1960–61)	73 (136)	Declining	(8)

*(1) Stephenson 1978, Alaska Fed. Aid Wildl. Rest. Prog. Rep. Project W-17-3.
(2) Pimlott *et al.* 1969.
(3) Van Ballenberghe *et al.* 1975.
(4) Stephenson and Van Ballenberghe 1978, Alaska Fed. Aid Wildl. Rest. Prog. Rep. Project W-17-8.
(5) Bjorge, R.R.; Myers, S.; Gunson, J.R. 1979, Alberta Fish and Wildl. Div., unpubl. rep.
(6) Rausch 1967.
(7) Rausch 1969.
(8) Kelsall 1968.
(9) Stephenson and Sexton 1974, Alaska Fed. Aid Wildl. Rest. Prog. Rep. Project W-17-8.

7. Determination of wolf densities

Having examined rates of increase and numerical trends of wolf populations generally in relation to food resources, densities, and exploitation rates, we now consider the special case of stationary populations where $\bar{r}$ is at or near 0. These populations should provide an insight into what ultimately determines density in the wild. Time-specific estimates of density in non-stationary populations exhibited 19-fold differences (Tables 3 and 4) and, although analytically useful in several ways, reveal little about what sets upper limits to population growth.

Table 7
Relationship between rate of human exploitation of wolf populations in North America and ensuing population trend

Location	No. of winters	Overwinter kill by humans (%)	Ensuing population trend	Data sources*
Alberta (Fort McMurray)	1 (1975–76)	10	Increasing	(1)
Minnesota (Northeastern)	1 (1970–71)	20	Stationary	(2)
Alaska (Interior: GMU 20A)	1 (1973–74)	21	Stationary	(3)
Ontario (Algonquin Park)	2 (1957–59)	27	Stationary	(4)
Alaska (South-central: GMU 13)	1 (1975–76)	29	Stationary	(5)
(Interior: GMU 20A)	1 (1974–75)	38	Stationary	(6)
Alaska (South-central: GMU 13)	2 (1976–78)	38	Declining	(7)
North-central Canada (Barren-ground caribou range)	1 (1954–55)	41	Stationary?	(8)
	1 (1955–56)	58	Declining	(8)
	1 (1960–61)	59	Declining	(8)
Alaska (Interior: GMU 20A)	1 (1975–76)	61	Declining	(6)
(South-central: Sustina River Study Area)	3 (1975–78)	64	Declining	(7)
North-central Canada (Wood Buffalo National Park)	2 (1952–54)	70	Declining	(9)

*(1) Fuller and Keith 1980.
(2) Van Ballenberghe *et al.* 1975.
(3) Stephenson 1978, Alaska Fed. Aid Wildl. Rest. Prog. Rep. Project W-17-3.
(4) Pimlott *et al.* 1969.
(5) Stephenson and Van Ballenberghe 1978, Alaska Fed. Aid Wildl. Rest. Prog. Rep. Project W-17-8.
(6) Haggstrom and Buchholtz 1978, Alaska Fed. Aid Wildl. Rest. Prog. Rep. Project W-17-9; Stephenson 1978 (*op. cit.*).
(7) Ballard and Spraker 1979, Alaska Fed. Aid Wildl. Rest. Prog. Rep. Projects W-17-9 and W-17-10.
(8) Calculated from mean density of 375 km^2/wolf in Arctic environments [Clark 1971, 311 km^2; Parker 1972, 513 km^2; Weeden 1976, 286 km^2; Stephenson and Van Ballenberghe 1978 (*op. cit.*), 389 km^2], the annual kill of wolves reported by Kelsall (1968, Fig. 14) on 1 554 000 km^2, and a rate of decline with intensive control efforts of 21% annually from 1955–56 to 1961–62 (based on decline in total kill).
(9) Fuller 1954, CWS unpubl. rep.

Densities of wolves in seven stationary populations ranged from 2.7 to 41.7/1000 km^2 (375 to 24 km^2 per wolf) and were unrelated to rates of exploitation (Table 8). There was, however, a highly significant correlation ($r = 0.94$, $P < 0.01$) between wolf densities and total ungulate biomass (Table 8 and Fig. 3). Furthermore, per-capita ungulate-biomass indices for these stationary populations were consistently low (96–328), and their mean of 206 was near the mean of 189 for three increasing populations noted earlier (Table 3) whose observed rates of increase were lowest. A declining malnourished wolf population in northeastern Minnesota evidently had per-capita biomass indices below 80 (Mech 1977*a*, Mech and Karns 1977).

The above analysis, coupled with that in previous sections, strongly suggests that wolf densities tend to adjust to available food resources, with rates of increase declining to 0 as per-capita food supplies decline due to either increasing numbers of wolves or decreasing numbers of ungulates. Where human exploitation is not excessive (<38% of fall numbers or, more likely, ≤30%, as discussed later), so much of the variation in rates of increase and wolf densities is accounted for by nutrition that other factors seemingly play a comparatively minor role. I therefore believe that Van Ballenberghe *et al.* (1975) were correct in concluding:

> Despite the documented existence of evolved mechanisms designed to lower the productivity of dense wolf populations, we believe that the available evidence indicates that environments rich in food lower the threshold of such mechanisms and are the ultimate factor accounting for the existence of dense wolf populations.

8. A summary of wolf population dynamics

The following synopsis of wolf population dynamics is based on conclusions drawn earlier in this paper, and on information previously reviewed by others. It attempts to outline in the briefest possible way the key interactions that control wolf populations — a controlling factor being one that influences rates of increase through impacts on rates of birth, death, or movement (Keith 1974). Such influences may or may not be density-dependent (regulatory).

Three factors dominate wolf population dynamics — wolf density, ungulate density and vulnerability, and human exploitation (Fig. 4): these are linked through wolf predation, social behaviour, and functional and numerical responses.

In a recent review, Packard and Mech (1980) stressed the apparent dependency of many behavioural constraints to population growth on available food resources:

> ... social behaviour often seems to be the proximate cause of numerical change which is ultimately controlled by food.

They described how various social factors dampen rates of numerical change, cause lags in numerical responses to fluctuating food supplies, and affect the nutritional status of certain cohorts. It was clear from Packard and Mech's (1980) review that both wolf and ungulate densities greatly influence social behaviour; but significant direct effects of human exploitation on social behaviour, though suspected (Woolpy 1968), have not to my knowledge been shown.

Functional (dietary) responses by predators to prey-density changes are major determinants of numerical responses and hence of predator densities. Such functional responses may be a direct consequence of fluctuating prey vulnerability, and involve changes in both prey vulnerability and percentage utilization of kills (Stenlund 1955, Pimlott *et al.* 1969, Mech *et al.* 1971, Peterson 1977). Alternatively, functional responses may be mediated through social behaviour that affects (1) prey vulnerability in buffer zones between pack territories and (2) wolf activity levels and thus total food requirements (Packard and Mech 1980). While functional responses have a major effect on numerical (demographic) responses, the latter are also affected by direct impacts of social behaviour on reproduction, survival, and dispersal

Figure 3
Relationship of wolf densities in seven stationary populations to the total biomass of ungulates present (data from Table 8)

Figure 4
A conceptual model of wolf population dynamics

Figure 3

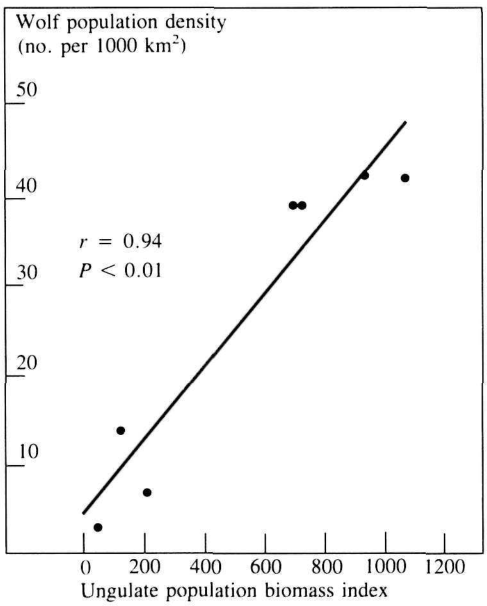


Figure 4

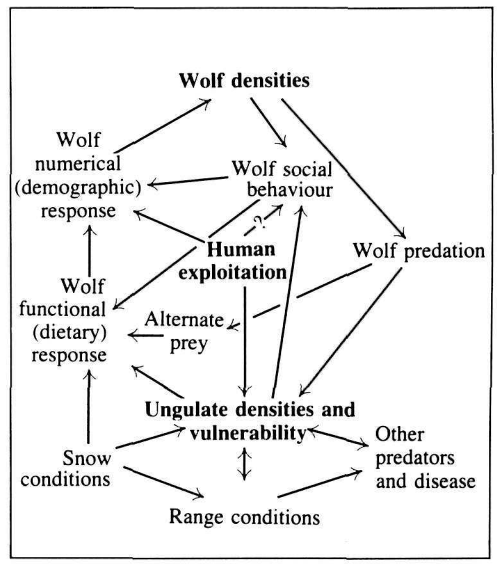


Table 8
Relationship of wolf densities in stationary populations to rates of exploitation and ungulate abundance

Location	Exploitation rate (% kill overwinter)	Wolf density (no. per 1000 km²)	Ungulate biomass index (per 100 km²)	Ungulate biomass per wolf	Data sources*
Minnesota					
(Northeastern)	20	41.7	933	224	(1)
Michigan					
(Isle Royale)	0	41.7	1090	258	(2)
Ontario					
(Algonquin Park)	27	38.5	670	174	(3)
(Algonquin Park)	0	38.5	670	174	(3)
Alaska					
(Interior: GMU 20A)	21–38	13.2	126	96	(4)
(South-central: GMU 13)	29	6.5	214	328	(5)
North-central Canada					
(Barren-ground caribou range)	0?	2.7	50	188	(6)

*(1) Van Ballenberghe *et al.* 1975.
(2) Krefting 1951, Mech 1966, Peterson 1977.
(3) Pimlott *et al.* 1969, Theberge and Strickland 1978.
(4) See footnotes (3) and (6), Table 7.
(5) See footnote (4), Table 4.
(6) See footnote (6), Table 4.

(Packard and Mech 1980) and by rates of human exploitation (Table 7).

Most regional wolf populations depend primarily on a single ungulate species during the winter, even if two or more are available (Carbyn 1975*a*, Fritts and Mech 1981), and marked declines in the usual food source precede any shift to alternate species (Mech 1977*b*, Theberge and Strickland 1978). In summer, beaver (*Castor canadensis*) are often important alternate prey, and major differences in wolf summer diets between regions and years have been linked to their relative availability (Pimlott *et al.* 1969; Voigt *et al.* 1976; Peterson 1977; Theberge and Strickland 1978; Carbyn 1980, unpubl. CWS rep.)

An alternate prey species whose significance has not been fully evaluated is the snowshoe hare (*Lepus americanus*). It occurs throughout the boreal forest, exhibits extreme periodic abundance, and unlike the beaver is available year-round. There are suggestions in the literature that hare abundance may play an important part in pup survival, especially when other prey are scarce (Rausch 1969; Mech 1977*a*; Stephenson and Van Ballenberghe 1978, unpubl. rep.).

To summarize, wolf population dynamics are largely dictated by the per-capita biomass of the ungulate food resource, as determined by wolf and ungulate densities and rates of human exploitation. The effect of food supply on wolf demography is influenced to an important extent by social behaviour, through effects on both functional and numerical responses. Alternate prey species are used most during summer.

9. The wolf's potential to affect ungulate numbers

The impact of predation is determined by combined numerical and functional responses of predators to prey densities. The demographic components of total numerical response culminate in a rate of increase, whose maximum (r_m) I earlier estimated to be about 0.304 (λ_m = 1.36) for wolves. This is higher than the observed ($\bar{r}$) or potential (r_p) rates of increase for either moose or caribou populations with adequate food and no large predators (Table 9), and is within the 0.29–0.58 range for white-tailed deer.

Two significant components of wolf functional response are, first, a variable consumption rate (up to 3-fold) without notable demographic change (Mech 1977*b*), and second, a tendency toward "wasteful" killing when ungulates are abundant or otherwise vulnerable (Pimlott *et al.* 1969; Mech *et al.* 1971; Peterson 1977; Carbyn, pers. comm.). The first characteristic helps to forestall numerical response by wolves to prey population declines; the second tends to elevate kill rates (kills per wolf in each unit of time). Their joint effect is to broaden the range of ungulate densities over which a given rate of predation (percentage of prey population killed) can be maintained by wolves without any numerical response.

The logical outcome of combining these numerical- and functional-response characteristics would be strongly density-dependent (regulatory) predation. The obvious lags in both types of responses, however will tend to generate recurrent fluctuations within the system (Krebs 1972, pp. 200–208; May 1976).

Errington's (1946) view that predators mainly take vulnerable surpluses from prey populations gained wide acceptance as a principle of population ecology. Its validity has been increasingly challenged, however, particularly in relation to predation by large carnivores on ungulates (Pimlott 1970; Bergerud 1974, 1979; Keith 1974; Mech and Karns 1977). There now seems little doubt that: (1) wolf predation is a major component of total annual mortality in many ungulate populations, (2) such losses are often largely additive to other kinds of mortality, and (3) wolf predation is therefore a significant controlling factor and may at times be regulatory.

Table 9
Rates of increase observed in ungulate populations with adequate food and no large predators

		Mean annual rates of increase calculated				
		from successive population estimates		from other demographic data		
Species	Location	Exponential ($\bar{r}$)	Finite ($\bar{\lambda}$)	Exponential (r_p)	Finite (λ_p)	Data sources*
Moose	Sweden	–	–	0.29	1.33	(1)
	Alberta (Elk Island Natl. Park)	0.26	1.30	–	–	(2)
	Alaska (Kenai Peninsula)	0.24	1.28	–	–	(3)
	Newfoundland (Anguille Mountains)			0.24	1.27	(4)
	(Entire province)	0.18	1.20			(4)
	Alberta (Rochester)	–	–	0.16	1.17	(5)
	Michigan (Isle Royale)	0.14	1.15	–	–	(6)
	Means	0.21	1.23	0.23	1.26	
Caribou	Newfoundland (Brunette Island)	0.35	1.41	–	–	(7)
	Alaska (St. Matthew Island)	0.30	1.35	–	–	(7)
	(Kenai)	0.27	1.31	–	–	(7)
	(Adak Island)	0.25	1.28	–	–	(7)
	(St. George and St. Paul Islands)	0.24	1.27	–	–	(7)
	Means	0.28	1.32			

(cont'd)

Table 9 *(cont'd)*

White-tailed deer	North Dakota (Mean for seven Natl. Wildlife Refuges)	0.58	1.79	–	–	(8)
	Michigan (George Reserve)	0.55	1.73	–	–	(9)
	Wisconsin (Necedah National Wildlife Refuge)	0.40	1.50	–	–	(10)
	Michigan	–	–			
	(Cusino Wildlife Experimental Station)	–	–	0.41	1.50	(11)
	(George Reserve)	–	–	0.35	1.42	(12)
	Minnesota (Mud Lake National Wildlife Refuge)	0.29	1.33	–	–	(13)
	Means	0.46	1.59	0.38	1.46	

(1) Pimlott (1959); based on reported sustained yield of 25% of fall populations over large areas.
(2) Blood 1974, (Fig. 1): 1961–63 and 1964–67.
(3) Spencer and Hakala 1964: 1949–55, takes into account approximately 10% harvest of fall populations.
(4) Mercer and Manuel 1974: estimate for Anguille Mountains moose population based on a sustained mean harvest of 1 moose/2.12 km^2 during 1960–72 from a stationary population having a late-winter density of 1 moose/0.58 km^2. Estimate for entire province based on increase in numbers over 56 years from introduction of four individuals to "well in excess of 100 000".
(5) This is the calculated survival-fecundity rate of increase (r_s) for an age-stable population based on age-specific survival and reproductive rates given by Mytton and Keith (1981).
(6) Krefting 1974: 1945–48.
(7) Data summarized by Bergerud (1979).
(8) Cook 1945: 1935–44.
(9) Kelker 1947: 1928–33.
(10) Martin and Krefting 1953: 1939–46.
(11) Van Etten *et al.* 1965: based on reported sustainable yield.
(12) Eberhardt 1960: based on annual harvest and population trend, 1933–46.
(13) Krefting and Erickson 1956: 1939–49.

10. Some management implications

10.1. Exploitation of wolf populations

Wildlife management, whether to manipulate densities or harvests, frequently depends on a relationship between rate of increase and rate of exploitation. I interpret available information on wolf populations as indicating that rates of increase are primarily determined by per-capita food supplies, and that these are increased by overwinter harvests of wolves that reduce their densities. The consequent rise in reproduction and/or pup survival, and thus in potential rate of increase (r_p), can evidently compensate for removal by humans of about 38% of fall populations (Table 7).

If this 38% harvest occurred during a short period, it would signify that r_p = 0.478 (ln 100/62). However, wolves have usually been taken over several months; hence, a substantial annual harvest of 38% really implies a considerably greater potential rate of increase (see Caughley 1977, pp. 172–174). A more conservative estimate of sustainable harvest, 23% of fall populations, was calculated from: (1) my earlier estimate that r_m = 0.304; (2) an assumed constant rate of harvest over the 5 months November–March; and (3) a reproductive coefficient (m_x) of 2.30 (see Caughley 1977, pp. 172–175).

The above two estimates of maximum sustainable exploitation (23% and 38%) are admittedly rough, but probably bracket actual values. I would, therefore, become concerned about the status of wolf populations whose annual rates of harvest were exceeding 30%. This figure is considerably below the 50% or more suggested by Mech (1970, pp. 63–64) as required to reduce wolf densities.

Of management significance also is the fact that age ratios in wolf populations are not consistently related to numerical trends. Stationary populations, whether exploited or not, tend to have 40% pups by fall or winter, whereas both increasing and decreasing exploited populations have a higher percentage. In each case, the percentage of pups reflects recruitment adjusted to per-capita food supplies, but populations with high recruitment may still decline because of excessive rates of exploitation.

10.2. Significance of ungulate/wolf ratios

The dynamics of ungulate and wolf populations are strongly linked (Fig. 4), and management must take this into account. A question of particular importance is at what ungulate/wolf ratio will the annual increment to the ungulate population support the wolves? A rough estimate of that ratio can be calculated from a knowledge of the number of kills per wolf annually, the annual rate of increase of the ungulate population, and the proportion of the annual increment to the ungulate population removed by hunting.

Information on kill rates by wolves comes primarily from aerial observations of radio-marked packs during winter (Table 10). Packs dependent on moose averaged one kill per 4.1 days, or one kill per wolf every 43 days. This is about 8.5 moose per wolf each year, assuming that any tendency for the moose kill to drop in summer, due to reduced need or alternate prey, is offset by the much smaller size of moose killed (largely calves). Kill rates by wolves of white-tailed deer and elk (*Cervus elaphus*) appear to be similar, averaging 16.6 per wolf annually.

Finite rates of increase ($\bar{\lambda}$ and λ_p) of moose populations ranged from 1.15 to 1.33 in different regions (Table 9), whereas rates of increase for white-tailed deer were 1.33 to 1.79.

The annual ungulate kill per wolf that would stabilize an *unhunted* ungulate population is estimated by:

$$K = N(\lambda - 1) \quad [1]$$

where K = ungulate kill per wolf annually
N = ungulate numbers per wolf in spring before births
λ = finite rate of ungulate increase annually

The minimum number of ungulates required per wolf to prevent λ from falling below 1.0 in an unhunted ungulate population would thus be:

$$N = \frac{K}{(\lambda - 1)} \qquad [2]$$

If hunting removes a proportion of the annual increment to an ungulate population, the minimum number of ungulates required per wolf to prevent λ from falling below 1.0 would then be:

$$N = \frac{K}{(\lambda - 1)\,(1 - H)} \qquad [3]$$

where H = proportion of annual increment removed by hunting.

This presumes that wolf predation and hunting mortality are additive to, and not simply replacing, other mortality factors.

Table 10
Kill rates of wolves in winter on moose, and on white-tailed deer and elk

Location	No. of winters	Ungulate prey species	Mean kill rate in winter (no. days per kill)		Data sources*
			Per pack	Per wolf	
Michigan					
(Isle Royale)	3	Moose	3.1	47	(1)
(Isle Royale)	7	Moose	3.3	36	(2)
Alaska					
(South-central: GMU 13)	2	Moose	4.1	36	(3)
Alberta					
(Fort McMurray)	2	Moose	4.7	45	(4)
Alaska					
(South-central: GMU 13)	2	Moose	5.5	49	(5)
Means			4.1	43	
Ontario					
(East-central)	1	White-tailed deer	2.2	18	(6)
Manitoba					
(Riding Mountain	1	Elk	3.6	14	(7)
National Park)	1	Elk and white-tailed deer	6.9	21	(7)
Minnesota					
(Northwestern)	4	White-tailed deer	7.0	32	(8)
(Northwestern)	5	White-tailed deer	7.8	25	(8)
Means			5.5	22	

*(1) Mech 1966.
(2) Peterson 1977.
(3) Calculated from data given by Ballard and Spraker (1979) (see footnote 7; table 7) for three packs that consumed mainly moose and for which data were allegedly most reliable; approximately 2/3 of recorded kills were during October–April.
(4) Fuller and Keith 1980.
(5) Stephenson and Van Ballenberghe 1978 (see footnote 5, Table 7), Burkholder 1959.
(6) Kolenosky 1972.
(7) Carbyn, in press. Two moose included in elk-kill rate.
(8) Fritts and Mech 1981: reportedly minimum estimate.
(9) Mech 1977*b*.

Required moose/wolf and deer/wolf ratios at different rates of increase and harvest are shown in Figures 5 and 6. Thus, a moose population with λ = 1.20, and half of its annual increment removed by hunting, needs a ratio of 85 moose per wolf to remain stationary. Without hunting, a ratio of 43:1 would suffice.

A recent study on 25 000 km^2 near Fort McMurray, Alberta, indicated a population of 4600 moose and 166 wolves (Fuller and Keith 1980, Hauge and Keith 1981). The moose were declining (λ = 0.78) and the wolves were increasing (λ = 1.21). Hunters were removing about 400 moose annually, or approximately half the annual increment to the moose population, whose potential finite rate of increase was about 1.17. According to the above model, the moose/wolf ratio needed to produce a stationary moose population would be 100:1. If hunting were stopped, the required moose/wolf ratio would be 50:1. The current ratio of 28:1 is far too high in either case and predicts a continued decline of moose. Stabilization of this moose population would necessitate a 44–72% reduction in wolf numbers.

Pimlott (1967*b*) calculated that an unhunted deer population with λ = 1.37 must outnumber wolves by 100:1 to remain stationary. Figure 6 indicates that a ratio of about 45:1 would be adequate. The main reason for the difference in these two ratios is that the consumption rates used in Pimlott's (1967*b*) calculations were equivalent to an annual kill rate of 36.7 deer per wolf, more than double the 16.6 observed in later field studies. As Mech (1970, pp. 183–185) noted, amounts consumed by wolves and other predators may be well above those actually required.

Relevant here also is the mean annual kill rate by each wolf of 16.6 deer compared to 8.5 moose, even though the average weight of a moose is around six times that of a deer. This approximately 3-fold difference in food biomass per unit time is probably a further reflection of the wolf's wide latitude in food consumption. I suspect that densities of deer and moose differed little within the boreal forest during pristine times. If so, a 2:1 ratio in annual rates of kill (16.6 deer as against 8.5 moose per wolf) would have produced a similar ratio of mortality

'igure 5
:ffect of potential rate of increase and rate of harvest m number of moose required per wolf to maintain a tationary moose population when each wolf kills 8.5 noose annually (see text and Tables 9 and 10)

Figure 6
Effect of potential rate of increase of harvest on number of white-tailed deer required per wolf to maintain a stationary deer population when each wolf kills 16.6 deer annually (see text and Tables 9 and 10)

Elk are a major prey of wolves in Jasper National Park (photo: L.N. Carbyn)

Figure 5

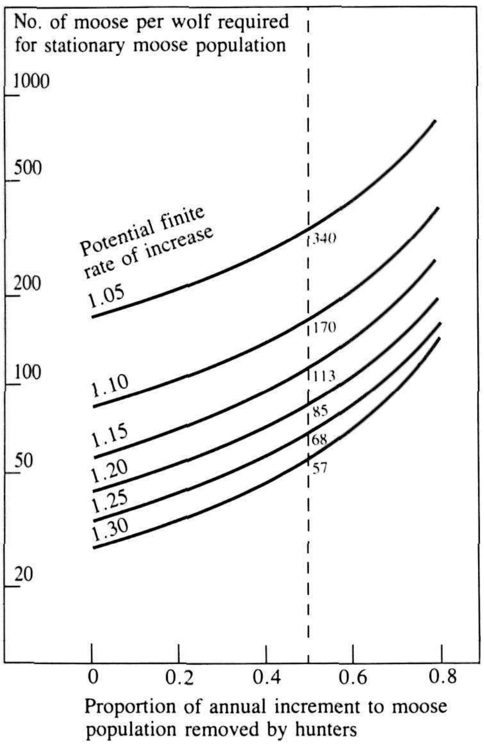
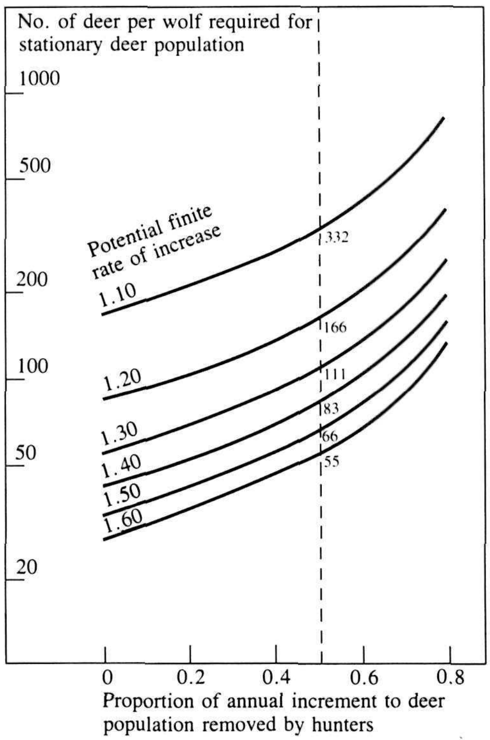


Figure 6



in their populations. It could therefore be significant from an evolutionary viewpoint, as well as for population regulation, that average rates of increase of deer and moose approximate this same 2:1 ratio ($\bar{r}$ = 0.43 vs. 0.22) (Table 9).

The families of curves depicted in Figures 5 and 6 are based on mean kill rates; they take no account of the potential variation in food consumption cited above, and are thus only first approximations, which must be interpreted cautiously. Increases or decreases in wolf kill rates would be directly and proportionately reflected in the calculated ungulate/wolf ratios.

11. Acknowledgements

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Social influences on reproduction in wolves

Wolves display a high degree of social interaction between members within family groups, and this has a significant influence on their general biology (photo: Scot Stewart)

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1. Abstract

The social behaviour of wolves has been viewed as having a regulatory function that adjusts population size to the carrying capacity of the environment by means of social stress occurring at high population densities. This view seemingly contradicts predictions based on individual selection, that genetically based traits causing individuals to be susceptible to continuous reproductive suppression could not persist in a population. Reproductive failure is frequent in both captive packs (an estimated 58–65% of adult females fail to reproduce each year) and wild packs (an estimated 38% of adult females fail to reproduce each year). A review of the causes of reproductive failure in captive packs indicates that lack of copulation is reported more frequently than suppression of gonadal cycles or stress-related pregnancy failure.

This study examines the relation between age and female reproduction in a captive colony. Young wolves in two captive packs were less successful during sexual competition than older wolves. The causes of reproductive failure appeared to be delayed behavioural maturation and stress due to absence of the opportunity to disperse. We suggest that the reproductive failure observed in wolves is a pattern of deferred reproduction that could have evolved by individual selection, meaning that future individual fitness is enhanced if individuals defer reproduction by remaining in a juvenile role within a pack. The effect of social behaviour on population regulation may be more a function of pack histories and compositions than of feedback between the population and its environment.

Our findings suggest that wolf packs and populations show an impressive tendency to maintain annual reproduction despite natural or artificial loss of current breeders. Models of natural or managed wolf populations should

consider individual pack history and social composition, and should allow for proliferation of new packs if food resources increase.

2. Introduction

It is widely accepted that in some wolf packs some adults do not reproduce (Mech 1970); however, the evolutionary explanation for this reproductive failure is not well established. Authors who viewed packs as hierarchical structures hypothesized that dominant individuals suppressed the reproduction of subordinates (Woolpy 1968, Rabb *et al.* 1967, Mech 1970). Presumably, observations of captive packs were consistent with the theory that in wild populations near the carrying capacity of the environment, reproductive suppression occurs as a response to social stress (Mech 1970, Van Ballenberghe *et al.* 1975). Group selection and/or kin selection has been invoked to explain social suppression of reproduction in wolves (Woolpy 1968, Haber 1977).

However, social behaviour of wolves does not appear to have as important a regulatory function as was previously proposed (Packard and Mech 1980). In this paper we shall review the evidence of reproductive failure and its causes in captive packs in order to evaluate the hypothesis of stress-related reproductive suppression. With data from our captive wolf colony, we shall examine the relationship between age and reproductive success, and the evidence for delayed behavioural maturity in two wolf packs that are family groups. Finally, we shall propose that reproductive failure in wolves may be better explained in terms of deferred reproduction than stress-related suppression and we shall discuss the implications of this theory.

The concept of deferred reproduction (Lack 1954, Geist 1968, Wiley 1974*a*) suggests that a physiologically mature individual will not exhibit sexual behaviour in a social environment where there is high sexual competition. Theoretically this trait would evolve when the expected fitness of individuals that defer reproduction is higher than that of other individuals that attempt to reproduce at the same age and under the same conditions. Thus, reproductive failure of young adults may be explained in terms of individual selection (Wiley 1974*b*, Wittenberger 1979), and group or kinship selection need not be invoked as has been done for wolves.

The importance of behavioural maturation as a factor influencing reproductive success in wolves has been mentioned previously (Rabb *et al.* 1967). Wild wolf packs are usually family groups composed of parents with offspring from several litters (Mech 1970). These offspring are thus in a social environment with high sexual competition. Studies of captive wolves suggest that offspring are probably less successful than their parents in sexual competition within family groups (Packard 1980, Zimen 1982).

2.1. Reproductive failure in captive packs

In this study, "reproductive failure" refers simply to lack of reproduction by an adult wolf during one breeding season of a pack, not to sexually immature individuals or individuals removed (or dispersed) from the natal pack. Sexual maturity is defined by the occurrence of ovulation in females and male testosterone cycles typical of breeding adults.

Reproductive failure of females in captive wolf packs is frequent (Table 1); however, following a change in social structure, previously non-reproductive pack members have bred within the packs (Rabb *et al.* 1967; Klinghammer, pers. comm.; Schotté and Ginsburg, pers. comm.; Packard 1980; Paquet *et al.* 1982). If each adult female in each breeding season is counted as a separate case, then failure to produce a litter was reported for 58% of 103 cases. Because eight of the litters produced did not survive, 65% of the cases were reproductively unsuccessful.

Table 1
Reproductive failure in captive packs

	♀♀/pack*		Litters/pack†			♀♀/year‡ Reproductive		Cause of failure‡§							
	1	>1	0	1	>1	Failure	Success	AE	AO	LP	LA	LR	CI	ME	PD
Rabb *et al.* 1967	0	8	0	6	2	19(2)	9	0	–	11	14	11	11	1	2
Lentfer and Sanders 1973	1	5	3	1	2	7	5	–	–	–	4	–	2	1	–
Altmann 1974	0	4	0	1	3	1(4)	4	1?	–	0	0	0	0	0	4
Zimen 1975, 1982	3	4	4	3	0	15	3	1	–	4	7	4	4	0	–
Fentress and Ryon 1982	2	4	1	1	4	11¶	13	–	–	–	–	–	1	4	–
Packard 1980	1	3	1	2	1	6(2)	2	0	1	1	3	0	2	3	2
Total	6	30	9	14	13	59(8)	36	2	1	16	28	15	20	9	8

*Number of breeding seasons when 1 or >1 pro-oestrous female was present in a pack.
†Number of breeding seasons when 0, 1, or >1 litter was born in a pack.
‡Cases include each breeding season of each pro-oestrous or adult female in pack. Parentheses indicate litters that died.
§Several causes were applicable in some cases. AE, anoestrous; AO, anovulatory; LP, low proceptivity; LA, low attractivity; LR, low receptivity; CI, courtship interruption; ME, metoestrous failure (after copulation, prior to parturition); PD, pup death.
¶Pups were found dead, but it was not clear that an entire litter was killed.

Reproductive failure could not be attributed to social stress in the cases where no litters were produced within a pack. This occurred in: (a) two packs consisting of littermates (Lentfer and Sanders 1973, Zimen 1982), (b) a pack in which potential breeders were hand-raised (Fentress and Ryon 1982), and (c) two packs with evidence of physiological pathology related to senescence or immaturity (Lentfer and Sanders 1973, Packard 1980).

Exclusive breeding by one female in a multi-female pack occurred only when the breeder was both dominant and pair-bonded. Exclusive breeders have been either the mother (Schotté and Ginsburg, pers. comm.; Packard 1980) or a sibling of the non-reproductive females (Rabb *et al.* 1967, Lentfer and Sanders 1973, Zimen 1982).

Clearly there is a high incidence of reproductive failure in captive wolf packs, but there is also evidence for successful reproduction during one season by more than one female per pack (multiple litters) in the absence of a dominant, pair-bonded breeder (Harrington *et al.* 1982). Multiple litters have been produced in packs in which (1) one member of the breeding pair had been removed (Rabb *et al.* 1967, Packard 1980, Fentress and Ryon 1982, Paquet *et al.* 1982), (2) there had been no previous reproduction among littermates (Rabb *et al.* 1967, Lentfer and Sanders 1973), or (3) the mother (initial reproductive female) was elderly (9 years) (Altmann 1974). There has been some variation in the number of consecutive years that multiple litters were produced in a pack following a disturbance such as removal of one member of the breeding pair.

In packs containing non-reproductive adults, the causes of reproductive failure must be examined to evaluate the hypothesis of stress-related reproductive failure.

2.2. Causes of reproductive failure

Failure may occur at any of several stages of the reproductive cycle, including endocrine and behavioural requisites for sexual solicitation (proceptivity), copulation, parturition, or rearing of offspring (Kleiman 1980). Theories of stress-related reproductive failure (Christian 1978) have typically concentrated on suppression of endocrine cycles due to adrenal-cortical activity.

Suppression of endocrine cycles in females is rare in captive packs (Table 1). In 1 (possibly 2) out of 61 cases, pro-oestrous vaginal discharge did not occur. One of those cases was an adult female that was severely injured (Zimen 1978), and the other was a yearling female described as "not fully mature" (Altmann 1974). Pro-oestrous discharge without ovulation was observed in a yearling female (Packard 1980) and an adult-sized wild female brought into captivity (Seal *et al.* 1979). There is no evidence for suppression of testosterone cycles in adult male wolves (Packard *et al.*, unpubl.).

Most studies have reported lack of copulation to be the primary cause of reproductive failure (Table 1). Low frequency of sexual solicitation, low attractiveness to males, rejection of males, and courtship interruption are frequently cited as reasons why individuals did not copulate.

Post-copulatory failure before birth has been reported in nine cases (Table 1). Four of these were inferred to be abortion (Fentress and Ryon 1982). Embryonic absorption of an entire litter has not been reported, although a female autopsied by Paquet (pers. comm.) had more placental scars than pups born in the corresponding litter. Causes of the remaining cases of failure were undetermined (Rabb *et al.* 1967, Lentfer and Sanders 1973, Packard 1980). Pups died in eight other cases, all involving young females.

Where reproductive failure is not due to age, but occurs as a result of aggression, it seems that it can be considered stress-related. Failure that is age-dependent and a result of intra-sexual competition (choice of mates by opposite sex) supports a hypothesis of deferred reproduction. This study examines the relationships among physiological maturity, behavioural maturity, and reproductive success in two captive wolf packs; the investigation was augmented by information on the reproductive cycles of wolves housed as pairs and singly.

3. Methods

3.1. Physiological maturity

Characteristics of the reproductive cycle were recorded for 16 female wolves at the US Fish and Wildlife Service wolf colony in Minnesota (Seal *et al.* 1979, Packard 1980). Observations were made during two reproductive seasons of some, but not all, of the females; thus, each season was considered as a separate case. There was a total of 23 cases (one case equals one female for one breeding season); 7 cases involved juveniles (10 months), 3 cases were yearlings (22 months) and 13 cases were adults ranging from almost 3 to 9 years old. Eight females were housed in two packs with initial sex ratios of 4:3 and 3:4 (females/males); pack composition changed in the second season to 4:2 and 2:2 (Fig. 1). Five females were housed as pairs with a male partner (females 322, 4, 38, 23, 52) and three were alone (females 34, 35, 37).

The wolves were anaesthetized during collection of physiological information (Seal *et al.* 1979). Physiological examinations occurred at weekly intervals for all females. In addition, females not housed in packs were examined three times a week from pro-oestrus through metoestrus.

Vaginal smears were examined for the presence of blood cells, cornified cells (Christie *et al.* 1972) and sperm. Vulvas were measured and examined for external signs of bloody discharge. Blood samples from the cephalic vein were analysed for oestradiol and progesterone (Seal *et al.* 1979). Progesterone levels above 10 ng/mL indicate ovulation in canids (Concannon *et al.* 1975). Abdominal swelling, hair loss, and lactation were recorded.

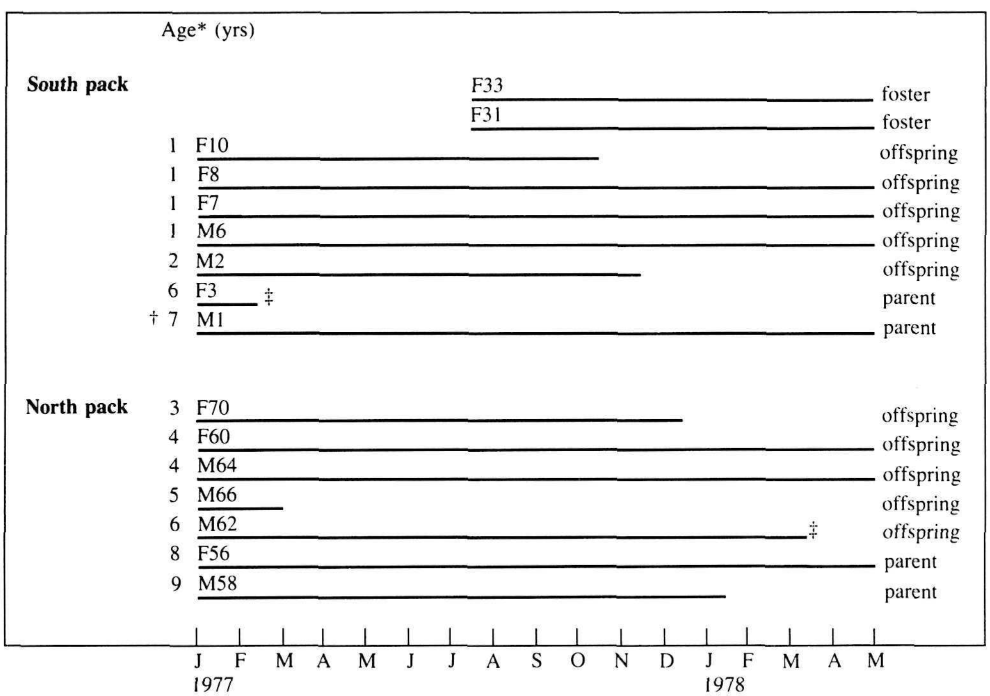
Behavioural observations were made daily (Packard 1980); female tail-aversion, male mounting, and copulatory ties were recorded. Behaviour of near-term females was checked at 4-h intervals for signs of denning or abortion.

3.2. Behavioural indices of maturity and stress

To characterize behaviour of pack wolves, indices of dominance (IDOM) and submissiveness (ISUB) were calculated. Values

Figure 1
Age, genetic relationships, and months during the study in which wolves were present in the pack (males M, females F)

Figure 1



* Age is noted as of May 1977.
† Age of M1 is uncertain because the wolf was caught in the wild.
‡ Indicates removal due to accidental causes (other than agonistic interaction) resulting in death or severe injury.

were the number of signals (behavioural acts) emitted minus the number of signals received. Behaviour frequencies were the total signals recorded (15-min sample periods) over 18 months (Packard 1980).

The following behaviour patterns were counted when calculating ISUB: curve-body, lick-intent, lick-up, roll (Packard 1980, Zimen 1982). Dominant behaviours counted in calculation of IDOM were: bite, chase, growl, lunge, nip, over-the-muzzle-bite, pin, stand-high, stand-over, sidle, flexed- or raised-leg-urination, scrape (Packard 1980, Zimen 1982).

ISUB was used as an indication of behavioural immaturity. Submission has been identified as a form of infantile behaviour persisting in adults after the function of food begging disappears (Schenkel 1967, Fox 1971). In the present study, submissive behaviour is viewed as a behavioural "tactic" (as used by Horn 1978) with the function of maintaining cohesive relationships, and may be shown by individuals of any age. This perspective is in accordance with theories of parent–offspring conflict and the potential use of signals to "manipulate" conspecifics (Dawkins and Krebs 1978). Individual wolves emitting more submissive signals than they received were considered behaviourally more immature than those receiving more than they emitted. Thus, behavioural immaturity in an adult may potentially indicate manipulation of other adults in the pack with the function of reducing aggressive tendencies that otherwise might force the individual to disperse.

IDOM was used as an indication of behavioural stress. Individuals that received more aggressive signals than they emitted were considered to be under more stress than those that emitted more than they received. The use of this index is thus consistent with Zimen's (1982) concept of dominance as based on the restriction of social initiative of less dominant by more dominant individuals. A dominant individual may not always emit the highest frequency of aggressive signals, but it does always receive the lowest frequency of aggressive signals.

These indices facilitated comparison of age-related differences in behaviour, independent of differences in behavioural rates between packs and among individuals. This concept of pack structure is a departure from a definition of dominance in terms of a rank hierarchy, and is based on the view that submissiveness and dominance are separate behavioural components (Schenkel 1967, Lockwood 1979, Zimen 1982).

4. Results

Characteristics of the reproductive cycle were determined for 23 cases (female/year) of which 21 were of known age (Table 2). Physiological maturity of individuals in successive seasons appeared to follow a sequence of stages with failure occurring at successively later stages in the reproductive cycle as the female matured.

In seven cases of juvenile females, no pups were successfully raised. Pro-oestrus did not occur in four out of seven cases. In two cases, juvenile females that copulated did not produce pups. One juvenile that produced pups did not raise them successfully.

No females between the ages of 2 and 4 years successfully raised pups ($N = 7$). In three yearling cases, reproductive failure occurred at the stages of ovulation, copulation, and post-parturition care of pups (details described by Seal *et al.* 1979, Packard 1980). Of the remaining cases, two females ovulated but did not copulate, one produced pups that did not sur-

Table 2
Characteristics of maturational stages in female wolves*

	Anoestrous					Pro-oestrous						No pregnancy				Pups died					Pups lived		
Female no.	7†	10†	34	35	322	7†	322	4	37	60†	70†	31†	33†	38	56†	8†	8†	23	23	52	52	56†	60†
Year	77	77	78	78	77	78	78	77	78	77	77	78	78	78	77	77	78	77	78	77	78	78	78
Age‡	1	1	1	1	>2	2	>3	2	4	4	3	1	1	6	8	1	2	4	5	5	6	9	5
Blood in smear	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Cornified cells	§	§	§	§	§	§	§	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Bloody discharge	–	–	–	–	–	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Oestradiol >10 pg	–	+	–	–	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	?
Swollen vulva	–	–	–	–	–	–	–	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Progest. >10 ng	–	–	–	–	–	–	–	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Oestrous behaviour	–	–	–	–	–	–	–	–	+	+	+	+	+	?	+	+	+	+	+	+	+	+	+
Mounted by male	–	–	¶	¶	–	–	–	–	¶	–	–	+	+	?	+	+	+	+	+	+	+	+	+
Copulation	–	–	¶	¶	–	–	–	?	¶	–	–	+	+	+	+	+	+	+	+	+	+	+	+
Abdomen swollen	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	+	+	+	+
Hair loss	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	+	+	+	+	+	+	+	+
Lactation	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	+	+	+	+	+	+	+	+
Denning behaviour	–	–	–	–	–	–	–	–	+	–	–	+	–	–	–	+	+	+	+	+	+	+	+
Parturition	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	+	+	+	+	+
Pup survival	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+

*"+", presence; "–", absence; "?", no data.
†Pack members.
‡In May following the breeding season.
§Fewer cornified than non-cornified cells present in vaginal smears.
¶No male present.

vive, and one ovulated but was not housed with a male.

Only adult females older than 4 years successfully raised pups (females 52, 60, 56). Three of the cases of adult reproductive failure were paired females (38, 23, 52) that had previously reproduced and shown full cycles (Packard 1980). The fourth case was a dominant female in a pack (female 56). Thus, causes of reproductive failure in adults were not related to social stress.

Comparison of indices of dominance and submissiveness (Fig. 2) suggests that cases of delayed behavioural maturation and of stress-related reproductive failure occurred. The original breeding members of each pack were distinctive in that they received more submissive and emitted more dominant signals than their younger offspring.

Three young females received more aggressive signals than they emitted; none of them reproduced. Two died before the second breeding season due to injuries inflicted by pack members (Packard 1980). The third was a yearling female that showed pro-oestrus without ovulation (F7).

Ages of six individuals with IDOM and ISUB values close to zero (equal number of signals emitted and received) varied from 10 months to over 6 years. The older offspring thus retained the behavioural characteristics of juveniles because their scores were more similar to younger siblings than to their parents.

Two aggressive young females with positive scores for IDOM also had positive scores for ISUB (emitted more signals than they received); thus they showed indications of behavioural immaturity but were not stressed. One of these females (juvenile F8) was the dominant female after the death of her mother, but she nevertheless did not acquire behavioural traits characteristic of older breeding individuals.

The eight offspring (4 males, 4 females) described above as behaviourally immature (non-negative ISUB scores) were physiologically capable of copulation although they had retained juvenile roles in the packs. In each pack, when one member of the breeding pair was removed (F3 in the South Pack and M58 in the North Pack), offspring that were not behaviourally stressed copulated with a parent and/or sibling of the opposite sex (Packard 1980).

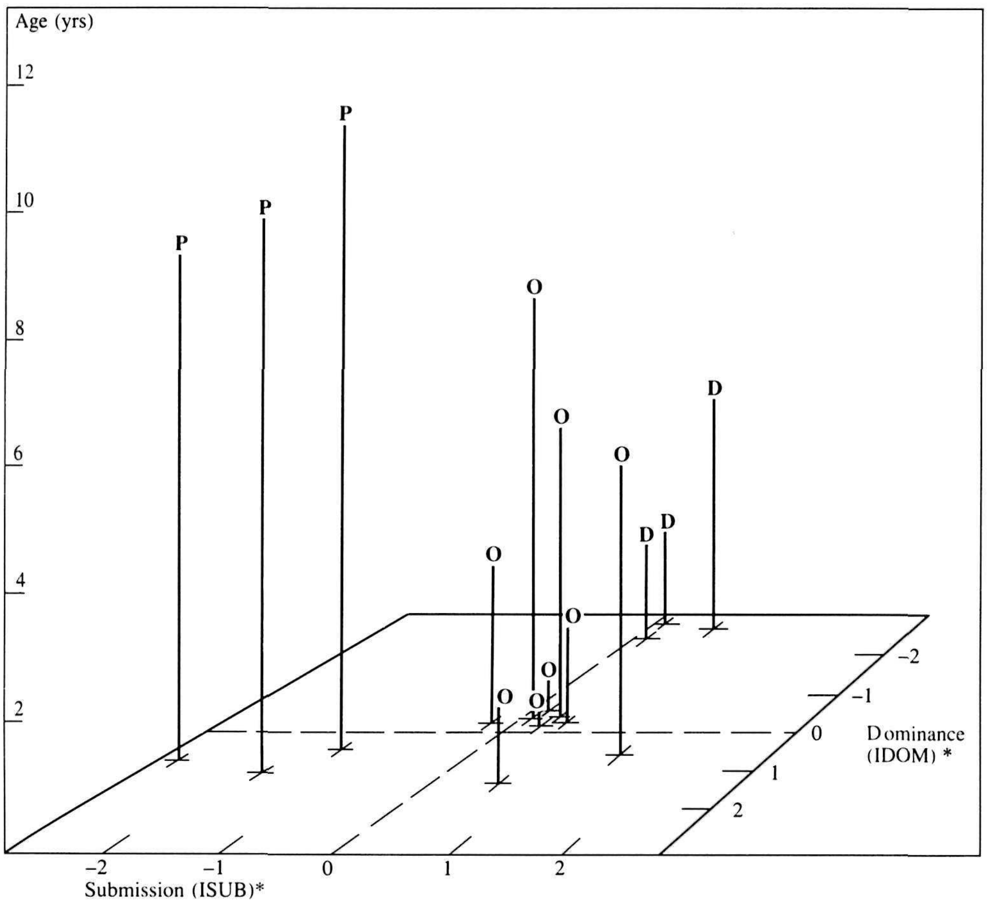
5. Discussion

5.1. Stress-related endocrine suppression

Reproductive suppression has been described as occurring when "animals who have sometimes already been sexually active are forced back by social circumstances into a state corresponding to that of an animal that has not yet reached sexual maturity" (Wickler 1972, p. 80). Although this distinction between suppression of mature individuals and the delay of maturation is not always made in discussions of reproductive suppression (e.g. Kleiman 1980), it is important in order to understand the evolution of wolf social behaviour.

Figure 2
Relation among indices of dominance (IDOM), submission (ISUB) and age, as of October 1977 or time of death

Figure 2



P parent
O offspring that bred
D non-reproductive offspring

* A positive value indicates more signals emitted than received; a negative value indicates more signals received than emitted.

In the present study, there was no evidence of suppression of endocrine cycles in adults due to stressful social circumstances. Six of the adult cases of failure were of females that were not housed in a pack and were thus not subject to social suppression. One adult pack female showed a complete ovulatory cycle despite the receipt of frequent aggression. The other two adult pack females that did not reproduce were not subject to social suppression (Packard 1980). Ovulation was suppressed in a subordinate yearling, but she had not previously ovulated and thus could not be considered mature.

In other studies, adults that have previously reproduced have occasionally lost the breeding role as a result of fights or loss of a mate (Rabb *et al.* 1967, Zimen 1982). Under captive conditions, such individuals are forced to remain in stressful social circumstances from which they could escape in the wild. Zimen (1976) identified potential dispersers by the distance maintained from the pack. Potential dispersers were of two types: former dominants who left voluntarily, and subordinates harassed by several members of the pack.

The high rate of reproductive failure in captive packs may not necessarily provide an entirely appropriate model for understanding social influences on reproduction in wild packs. In captivity there is no opportunity for dispersal, and social groupings may not necessarily be analogous to those found in the wild.

5.2. Deferred reproduction

The evolution of deferred reproduction has been discussed for a number of vertebrates (Wiley 1974*a*, Davies 1978). Mathematical analysis predicts a selective advantage to delayed reproduction when (a) it increases survival of pre-reproductive members of the population, and/or (b) individual reproductive success is improved by delayed breeding (Wiley 1974*a*, Wittenberger 1979). Delayed physiological or behavioural maturation or both occurs in several species with relatively high social tolerance (Geist 1968, Wittenberger 1979), as well as in those with high competition for mates or territories (Davies 1978).

To determine the adaptive advantage of deferred reproduction, one would ideally follow the lifetime reproductive success of individuals relative to age of first reproduction. However, such longitudinal data are not available for wolves. An alternative is to examine a cross-section of reproductive success of individuals of different ages.

In captive wolf packs (Fig. 3), the probability of pro-oestrus is low in 10-month-old females, but nearly all females reach puberty by 22 months. At least some individuals are capable of reproducing at 10 months (Medjo and Mech 1976). The probability of copulation or successul reproduction or both is higher in adults than in 22-month-old females. Thus, the probability of reproductive success is lower in juvenile and yearling wolves than in adults, for a variety of reasons.

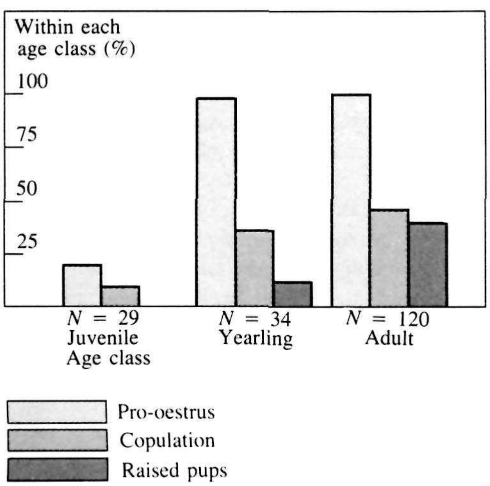
We suggest that the survival or reproductive success or both of offspring that attempt

Figure 3
Percentage* of females in three reproductive stages as a function of age: taken from cases reported in the literature (Table 1)

to reproduce within the natal pack in the presence of dominant parents is lower than of those that defer reproduction until the breeding-pair-bond is broken or the offspring disperse. Individuals susceptible to endocrine disturbance of reproductive cycles would be less likely to attain breeding status when the opportunity arose. Thus those that defer reproduction under adverse social conditions, but retain physiological readiness to breed, would theoretically have a higher genetic representation in future generations than those susceptible to physiological suppression.

In the present study, individuals with behavioural profiles indicating behavioural immaturity (as defined by intermediate values of ISUB and IDOM) were not in stressful social circumstances and did not reproduce in the presence of parents. However, when the parental pair-bond was broken, these individuals copulated. Thus we infer that an individual maintaining a juvenile role within a pack may appease the aggressive tendencies that force dispersal of individuals that do not maintain a juvenile role.

Figure 3



* Percentages represent the number of cases of age *N* showing characteristics of the reproductive stage, divided by the total number of cases of age *N*.

5.3. Flexibility in the mating system of free-ranging wolves

Harrington *et al.* (1982) found that the frequency of matings among more than one pair within packs containing more than one female was higher than has previously been implied in descriptions of the monogamous mating system of wolves. From reports of wild studies, they estimated that more than one litter per pack was born in 22–41% of packs with more than one adult female, implying that reproductive failure occurred in 59–78% of large wild packs. This estimate compares favourably with the proportion of captive packs with several adult females in which only one litter was born (61%; cf. Harrington *et al.* 1982), and the proportion of captive packs of all sizes in which one or no litter was produced (72% of 36 packs listed in Table 1).

However, if breeding seasons of individual adult females are counted rather than breeding seasons of packs containing several adult females, the frequency of reproductive failure in wild packs appears somewhat lower. It is difficult to obtain reliable data on individual reproductive success in the wild, but of the studies reporting such information, reproductive failure occurred in about 38% of 60 cases. This is lower than the estimated reproductive failure (58–65%) among captives (Table 1).

A possible explanation for the lower rate of female reproductive failure in the wild may be the prevalence of small packs initiated by dispersed wolves. No evidence of multiple litters per pack has been found in Minnesota studies (Van Ballenberghe *et al.* 1975, Mech 1977*a*). In a dense population with scarce prey, pack sizes were small owing to mortality and new breeding units were rare (Mech 1977*a*). In a low-density but growing population, pack sizes remained small due to dispersal of maturing individuals, which established new breeding units (Fritts and Mech 1981). It might be that under such conditions, individuals leave a pack rather than remain in a non-reproductive role.

Even in Alaska, where pack sizes are larger and multiple litters per pack are more frequent, more females are successful than unsuccessful (Ballard, pers. comm.). It has been assumed that larger packs occur where prey body-size is larger (Zimen 1976). If reproductive failure is seen as a function of sexual competition, then this would imply that females compete for mates because resources contained in the territory controlled by those mates are limited. Theoretically, where such resources are limited, tolerant females whose pups compete unsuccessfully with another litter would thus make a lower genetic contribution to future generations. However, where resources are abundant, such competition may not occur as suggested by Paquet *et al.* (1982).

When wild packs of all sizes are considered (Packard 1980), only one litter was born in 94% of 101 documented cases that were reviewed. This suggests that pack territories typically are able to support only one litter per year and indicates a high level of sexual competition among females within the same pack. Under conditions of high sexual competition, older females would appear to have a competitive edge over younger females. It is under such conditions that deferred reproduction would be predicted to evolve (Wiley 1974*b*).

5.4. Management implications

The view that reproductive failure in wild wolf packs is more a function of deferred reproduction than of stress-related suppression has several implications regarding management of wolf populations. One of the most important is that if an alpha pack member is killed, a "bider" (a sexually mature, non-breeding subordinate) can almost immediately assume the breeding role because it is physiologically capable of doing so. All that is required is a shift in the individual's social status; the loss of an alpha could be compensated at almost any time during the reproductive cycle, including the oestrous period. This fact increases the chance that each wolf pack will reproduce every year despite a certain amount of harvesting.

Furthermore, even if pack alphas or biders are removed, transient lone wolves, which may comprise as much as 28% of a wolf population (Mech 1970), can either be integrated into packs as breeders (Packard and Mech 1980), or can pair with other loners when sufficient space and resources are available, reproduce, and produce their own packs (Fritts and Mech 1981).

It has been suggested that a higher proportion of females may reproduce in a hunted population than in a non-hunted one if hunting disrupts pack stability by removing previously reproductive individuals (Haber 1974, Van Ballenberghe *et al.* 1975, Pulliainen 1982). Our results might be construed as lending evidence to this suggestion. However, most wild wolf packs consist primarily of several pups, a breeding pair, and only one or two biders. Only packs numbering more than about 10 members in midwinter would usually contain more than one or two biders of each sex that even potentially could constitute "extra" breeders if an alpha were killed. In the relatively rare larger packs containing more than two potential breeders of each sex, we would expect that even if more than one pair did breed, competition for resources would usually result in domination by one pair. Therefore we would not predict continued reproduction by more than one female in a pack for a long period following disturbance due to hunting.

Where there are enough resources either to support more than one litter in a pack or to establish an additional pack, it would be difficult to distinguish the effects of harvesting from the natural processes resulting in pack splitting. Even without harvest, packs may split into separate groups, subordinate members might disperse and begin new packs (Fritts and Mech 1981), or occasionally two pairs within a pack may both raise litters (Harrington *et al.* 1982).

We have focused on the relation between age and reproductive success, partly because age-specific reproduction is an important component required for modelling population dynamics of long-lived species. Although we conclude that younger wolves have a lower probability of successful reproduction within a pack, reproduction does not appear to be a simple function of age. Social influences on reproduction in wolves cannot easily be separated from social influences on dispersal, mortality, and immigration. In addition, food availability and population density interact with intra-pack social factors in determining the proportion of reproductive individuals in each age class (Packard and Mech 1980).

Ideally, the history and composition of each pack would be considered in predicting changes in a wolf population. For example, a pack with young offspring would be predicted to be more stable than one with offspring of peak reproductive age. The apparent stability of the Isle Royale wolf pack during the 1960s may thus have been more a function of the age of the pack and the consistent availability of prey than of the density-dependent mechanisms of population regulation. Changes in wolf populations on Isle Royale (Peterson 1977) and in Minnesota (Mech 1977*a*) suggest that social factors may buffer pack and population responses to changes in prey populations.

Incorporation of knowledge regarding wolf social behaviour into models predicting population change is still in an initial stage. A qualitative model describing the feedback between ecological factors and pack size was proposed by Zimen (1976). Zimen accepted the generalization that only one pair of wolves breeds within a pack, and therefore considered mating behaviour of minor importance in predicting changes in pack size. A quantitative model of predator–prey interactions in Denali National Park was proposed by Haber (1977). In Haber's model, the number of litters born into a pack is a function of pack size. When a pack contains more than 15 wolves, the model increases both the probability that an additional litter would be produced, and the probability of pack splitting and consequent mortality of dispersing wolves.

The results of our study suggest that specific models based on knowledge of social and ecological factors in a given wolf population may provide more accurate predictions than generalized models. In contrast to the density-dependent approach used by Haber (1977) we would recommend a model that considers the history of individual packs and that can handle the probability of new reproductive units being established within a population (Fritts and Mech 1981).

Ultimately we hope that detailed studies of the variability of wolf packs in the wild and in captivity will contribute to generalizations about the behavioural tactics of individuals confronted with changing ecological and social conditions as outlined by Zimen (1982). The complexity of social influences on reproduction in wolves illustrates the difficulty of determining the mechanisms of density-dependent feedback on the population growth of long-lived species living in monogamous family groups.

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Considerations in wolf management related to genetic variability and adaptive change

John B. Theberge

1. Abstract

Characteristics of wolf ranges in the future may be increased patchiness in the distribution of prey populations, and lower prey densities due to human impacts. The genus *Canis* has demonstrated a low rate of speciation attributed in the literature to characteristics that require allopatric conditions for speciation to occur. The wolf has, however, a wide genetic variability. This variability may have been moulded not only by limited allopatric conditions but by partial genetic isolation without geographic barriers, resulting in subspeciation. Differences in dispersal and vagility in wolves occur when populations are low or high in relation to food supply, hypothetically balancing allopatric and non-allopatric conditions. Adaptive changes through genetic isolation may be too slow in K-selected wolves to keep up with environmental change. Consequently, wolf management should aim at maintaining some gene flow among local demes. Loss of genetic variability through inbreeding in small genetically isolated populations also argues for attempting to maintain gene flow. Factors influencing minimum population size are discussed. Future wolf management must guard against an increasingly patchy distribution of wolves by preventing regional prey depletion or long-term wolf control, and maintaining a management perspective over very large areas of land.

2. Introduction

This paper relates wolf management to theoretical and speculative rather than empirical active forefronts of inquiry into modes of speciation and population genetics. "No one yet has observed the development from beginning to end of a new plant or animal species in nature" (Bush 1975). As well, divergent opinions exist in the literature about the adaptive consequences of inbreeding. Thus, this paper is speculative. I have attempted to bridge a gap between applied population ecology and population genetics in the hopes of generating more mutual concern, in the interests of wildlife conservation.

The purpose is to explore some implications for the conservation (wise management) of the wolf (*Canis lupus*) in relation to its genetic potential for adaptive change, and the risks of reduced genetic variability. These two topics will be examined in reference to the literature on modes of speciation and the genetics of small populations, respectively.

Wildlife management has seldom taken account of genetic fitness, especially in long-lived species, even though "any strategy for the conservation of a particular species should, in part, be determined by knowledge (or inference) about the genetic structure of that species" (Franklin 1980, p. 135).

The wolf has been referred to as one of the most adaptable species (apart from man) in the world (Rutter and Pimlott 1968; Goldman 1944, p. 389). Yet the wolf has been unable to cope with environmental effects of agriculture and urbanization, which together with direct killing have removed it from half its historic North American range. The remaining North American wolf range will probably not be so radically transformed, but one can foresee a significant increase in resource extraction, with accompanying increases in human populations. There will be increasing demands for big game hunting. The result will be a trend to greater patchiness in the distribution of predator and prey populations and, where mortality factors on ungulates are non-compensatory and primarily additive, to lower prey densities. This trend to regional prey depletion, in which human hunting is at least partially implicated, is obvious already from a number of major declines: caribou and moose in northern BC and central Alaska, caribou in the Alaskan western Arctic, moose in Ontario, bison in the Slave River lowlands, and deer on Vancouver Island and in Québec. It is to such a future that the wolf must adapt.

3. Potential for adaptive change

The wolf's historic distribution in North America extended across every biome and was the widest of any mammalian species (Young 1944). As a predator of large mammals, the wolf is an ecological generalist, with the concomitant wide adaptability attributed to generalists (Van Valen 1965). This wide adaptability may be due to a low rate of speciation within the genus *Canis*, a suggestion supported by the observation that all species of *Canis* that have been karyotyped have a chromosome number of $2N = 78$ (Matthey 1973, p. 563). A narrow range in chromosome number is an indicator of a low rate of speciation (Bush 1975, p. 341). This low rate in genus *Canis* has been attributed to its mode of speciation by allopatry, the tendency of geographic barriers to restrict gene flow (Bush 1975). Bush described allopatric speciation as a relatively slow process, characteristic of species with spacing behaviour selecting dispersal, extensive home ranges, generalized feeding habits, K-strategists, and high "vagility" [meaning freedom to move about but defined by White (1978, p. 18) as "mean distance in a straight line between the points at which an individual is born and dies"].

Although speciation has been slow in *Canis*, there are 23 subspecies of *Canis lupus* described for North America (Young 1944). Among Canadian mammals, the wolf has the second highest number of subspecies — 17 (Banfield 1974). Five other Canadian mammalian species with large numbers of subspecies are all rodents, characterized by very low vagility and r-strategies, both factors leading to rapid speciation (Bush 1975, p. 342). Although Jolicoeur (1959) concluded that too many subspecific names are probably in use for the wolf, there is clearly a great deal of morphological and behavioural variability within the species. The source of this variability may in part be hybridization among members of the genus *Canis* during the Pleistocene era; then at least four large species were present in North America (Nowak 1978, pp. 7–8). Contemporary hybridization resulting in viable offspring has been described among many *Canis* species (Gray 1972, pp. 45–51), no doubt facilitated by a common diploid chromosome number. This explanation is, of course, speculative.

This variability may also have been moulded by more than just the limited allopatric process described by Bush. The characteristically high rates of dispersal and high vagility of *Canis*, as noted by Bush, are valid when wolf populations are low in relation to food availability. However, in dense populations few wolves disperse long distances; vagility is low, given their mobility; and packs reproduce as small

Social behaviour of wolves in summer centres on the raising of pups (photo: W.C. Mason)

semi-isolated demes (Mech 1970, p. 50). These characteristics are prerequisites for speciation without geographical barriers, of which a number of types have been described recently. Speciation may occur across a genetic cline along a geographical gradient, called "clinal speciation" (White 1978) or "parapatric speciation" (Bush 1975). Or it may occur in sympatric populations under "stasispatric conditions", described as a restriction in gene flow due to the presence of small social units with partial inbreeding, such as "when a family group becomes isolated temporarily from the main population, e.g. in a valley or at the periphery of the range" (Wilson *et al.* 1975). Thus, one can envision a balance of sorts between conditions conducive to allopatric speciation operating in part at times in wolves, especially when populations are dense, leading to subspeciation but not to full speciation because of the counteracting influences of generalized food habits, K-strategies, and periodic high amounts of dispersal and vagility when populations are low.

What are the implications of these processes, which cause variations in gene pools, for the future of wolves experiencing patchier prey distributions and reduced prey densities? These environmental conditions will result in increased genetic isolation, either socially or geographically, leading to more rapid variation in local demes. This trend might be viewed as beneficial, by creating more habitat-specific adaptations. However, in a long-lived species such as the wolf, local changes in gene frequencies may not be able to occur rapidly enough to meet local or regional environmental changes. Man's activities in northern environments have rapidly altered the prey-base for wolves in many areas through habitat change, e.g. as a result of logging the boreal-hardwood ecotone of central Ontario, and hunting. Hunting by wolves, although largely learned, must include a genotypic component (Mech 1970, p. 138) in such traits as sensing prey, response to stimuli such as running (Mech 1970, p. 201), and possibly even in social structure such as pack size, which varies with size of prey animals (Mech 1970, pp. 39–43). Changing to buffer prey species may not occur as rapidly as changes in prey availability, as shown in Algonquin Park (Voigt *et al.* 1976, Theberge and Strickland 1978).

Thus, it seems prudent in the management of large mammals, such as wolves, that biologists aim at maintaining at least some gene flow among local demes to prevent genetic isolation. The spatial scale for the management of wolves must be large, not applied solely to local populations. Local areas of wolf disappearance due to lack of prey or severe wolf control are not to the genetic advantage of the species.

4. Risk of reduced genetic variability

As wolf populations become smaller and more patchy in distribution, the negative effects of inbreeding could potentially reduce genetic variability through loss of heterogeneity. Inbreeding is manifested through genetic drift in small populations (Wilson and Bossert 1971, p. 87). Other comments on deleterious effects of inbreeding are quoted below. "Inbreeding has deleterious effects on survival and reproduction, and affects such characters as growth rate and adult size" (Franklin 1980, p. 140). "Enough is known about inbreeding to justify concern that any increase in homozygosity reduces absolute vigor and fecundity" (Soule 1980, p. 160). "It is obvious that conservationists ought to view inbreeding as an anathema" (Soule 1980, p. 158).

Shields (1982), in contrast, draws attention to the literature describing beneficial effects of inbreeding arising from its capacity to faithfully transmit parental genomes that have proven themselves. He describes the need for cost/benefit assessments of inbreeding and suggests, apparently arbitrarily, that the range of balance for species with low fecundity may occur with breeding populations somewhere between 2 and 1000. Nevertheless, Shields does not share the concerns of Soule or Franklin about inbreeding, even where costs outweigh benefits because, in the wild, selection may theoretically cull out the maladapted homozygotes generated by inbreeding. Selection, however, is less rapid among K-strategists such as the wolf than among r-strategists. Any reduction in fecundity, a known consequence of close-kin matings (Soule 1980, p. 157), even short-term reductions, could be disastrous in small populations.

The extent of inbreeding in wolf populations is unknown. Immigration and emigration among packs in a dense population is limited by intolerant social behaviour and interpack aggression (Mech 1970, p. 50). Matings are known among litter mates or between parents and offspring (Mech 1970, p. 111). Wolves have a low fecundity, a characteristic that lowers resistance to inbreeding (Franklin 1980, p. 50). One percent inbreeding was taken by Soule (1980, p. 160) as a maximum acceptable level for short-term preservation programs. This represents 50 animals breeding freely among themselves, as the rate of homozygosity per generation through inbreeding is $1/2\ N_e$, where N_e is the size of the effective breeding population (Soule 1980, p. 160; Wilson and Bossert 1971, pp. 85–86). Soule remarked that even this low level of inbreeding occurring for 20 or 30 generations will result in a loss of about one-fourth of a population's genetic variation, along with much of its capacity to adapt to changing conditions. For long-term genetic fitness, Franklin (1980) proposed a minimum effective population size of 500. Using Soule's 1% rule, however, the census number of wolves necessary to maintain 50 breeding animals must be adjusted upward owing to a number of factors, including the proportion of the population that breeds, which in Table 1 ranges from 17 to 79% and is largely a function of degree of exploitation. Also requiring an upward adjustment of the necessary census number is the proportion of wolves that breed more than once and the effect of periodic depression in population size, as no wolf population is stable for long. Moreover, the greater the degree to which close-kin matings occur within packs, the more one would have to consider packs, rather than individuals, as breeding units, which would greatly inflate the necessary number of wolves. No data exist from wild populations to allow assessment of this last factor.

Table 1
Approximate proportions of breeding animals in various wolf populations*

Location	Status	Type of data	Approximate proportion of breeders	Reference
Michigan (Isle Royale)	Protected	Observation	0.17	Wolfe & Allen 1973, Allen 1979
Alaska (McKinley Park)	Protected	Observation	0.22	Haber 1977
Ontario (Algonquin Park)	Lightly exploited	Autopsy	0.45	Pimlott *et al.* 1968
Minnesota (North-eastern)	Lightly exploited	Capture	0.42	Van Ballenberghe *et al.* 1975
Alaska	Exploited	Autopsy	0.79	Rausch 1967

*Includes all animals more than 12 months old.

Without knowing exact numbers, it becomes clear that minimal size of a wolf population must be much larger than 50 animals, even to meet the short-range minimal "1% rule". Areal requirements for such populations are vast; wolf densities range from 1 wolf/26–130 km^2 in the boreal-hardwood ecotone to 1 wolf/520 km^2 in the eastern Arctic, and probably average approximately 1 wolf/260 km^2 for the Canadian wolf range (Theberge 1977). Theoretically, 50 breeding wolves at this average density would require 13 000 km^2. This calculation does not take account of all the factors that inflate the required number of wolves above 50.

From a wildlife manager's standpoint, this discussion of the negative effects of intensive inbreeding points to the same conclusions as previously made: that genetic variability is best maintained if some gene flow among local demes takes place and genetic isolation is avoided. Very little gene flow may be sufficient to counteract the effects of inbreeding (Shields, pers. comm.), but that occasional flow may be very important. The discussion also adds a numerical and spatial dimension to local demes, which for wolves are very large. Discrete populations occupying ranges from a few hundred to a few thousand square kilometres must be considered candidates for gradual reduction in genetic variability, particularly significant if environments change rapidly, as previously discussed.

Populations founded from a few individuals represent a relatively narrow genetic base; periodic re-introductions of additional wolves may be necessary to broaden this base. The same holds true for small partially isolated populations, such as on Isle Royale, if immigration does not occur naturally for long periods.

The implications of these concerns about genetic variability are relevant to wilderness park managers as well as wildlife managers. It is doubtful if any park or reserve in North America is large enough to accommodate a long-term genetically viable wolf population if the population is isolated, a conclusion also reached by Soule (1980, p. 163). Bigger parks and reserves are obviously better, but must be accompanied by co-operative management with adjacent wildlife and land-use agencies. Adjacent management may not necessarily require full protection for wolves because wolves demonstrate compensatory reproduction (Table 1). However, if wolf harvest is continuous or severe, it will tend to increase patchiness, with possible deleterious genetic consequences as discussed.

In summary, the theory on which wolf management is based must contain greater recognition of the need to guard against a future of increasingly patchy distribution, by preventing any regional prey depletion or long-term severe wolf control, and by maintaining a management purview over very large areas of land.

Genetic considerations in the management of the wolf and other large vertebrates: an alternative view

William M. Shields

1. Abstract

In nature wolves appear to be intrinsically philopatric. This limitation on dispersal results in the subdivision of wolf megapopulations into relatively small, random mating and semi-isolated demes, with little or moderate gene flow among demes. The observed genetic structure is consistent with the notion that wolves and other low fecundity vertebrates should be optimally inbreeding at some intermediate inbreeding intensity. Such a breeding population structure is likely to increase or maintain local adaptation, maintain or increase species-wide genetic variability, and so enhance a species' capacity to genetically respond to environmental flux via Wright's shifting balance processes. With respect to management, this may imply that wolf megapopulations should be maintained at high numbers, opportunities for naturally low levels of gene flow among neighbouring demes should be maintained or provided, and care be taken not to generate overwide outbreeding during the stocking of new populations in empty but suitable habitat.

2. Introduction

In this publication, Theberge clearly draws attention to the fact that perhaps too "little concern in wildlife management has focused on genetic" considerations. His comments are strongly grounded in Soule and Wilcox's (1980) attempt to begin remedying this situation. Soule and Wilcox have provided this impetus by drawing the views of a variety of experts into a single volume that attempts to provide a stronger genetic, and ultimately evolutionary, viewpoint for a more comprehensive conservation biology. Theberge's valuable contribution is an indication of Soule and Wilcox's success at initiating this important integrative process.

Following Theberge (and Soule and Wilcox), my purpose also is to explore current genetic and evolutionary theory in the hope of deriving implications that might be useful in the management of wolves (*Canis lupus*), and ideally other large vertebrates as well. In doing so, I shall draw attention to alternative interpretations of some of the arguments developed by Soule and Wilcox (1980) and elaborated by Theberge (this publication). Taken together, my criticisms and the alternative views associated with them may provide a grounding for different suggestions about the conservation of wolves and other large vertebrates.

3. Potential for adaptive change

Theberge makes the important point that "vagility (distinct from mobility, and defined by White (1978, p. 18) as 'mean distance in a straight line between the points at which an individual is born and dies')", is a primary determinant of population structure and thus of evolutionary potential. However, his assertion that wolves are characterized alternately by low vagility (in dense populations) and high vagility (in sparse populations), and thus changing population structure, fails to consider the importance of local densities in determining population structure. It is effective dispersal (absolute dispersal distances, i.e. vagility divided by average home range or territory diameters) and not vagility *per se* that determines deme size, and is thus a primary component of population structure (for reviews see Wright 1977, 1978; Greenwood 1980, Shields 1982).

As Theberge states, wolves are intensely philopatric when in dense populations in saturated habitats. There is little or no successful dispersal, with individuals usually remaining in their natal packs and often generating full-sib or parent-offspring pair bonds. Those few individuals that do attempt to disperse are usually prevented by the aggressive social intolerance of established pack members, which have been known to kill such dispersing "strangers" (Mech 1970, Fritts and Mech 1981). Such philopatry and social intolerance result in small (N_e <25), semi-isolated demes (= packs), and relatively high levels of inbreeding (Mech 1970, Shields 1982).

In contrast, Theberge suggests that wolves in low density populations are characterized by relatively high vagility. Although wolves do disperse out of their natal packs in such conditions, they often (4 of 7 cases) settle in suitable empty sites adjacent to their natal home ranges (Fritts and Mech 1981). Because territory sizes are much larger in sparse populations than in dense ones, those that disperse farther must move more impressive absolute distances as they pass occupied or unsuitable habitat before settling in the nearest suitable and unoccupied area. Despite the relatively long spatial distances involved, such wolves rarely move more than three or four home ranges from their natal or capture areas (Fritts and Mech 1981). Because density and pack size are low, and effective dispersal remains philopatric, the sparse, like the dense, population of wolves breeds in small (N_e <50) semi-isolated and therefore relatively inbred demes (though the probability of incest is lower).

The philopatric dispersal system characterizing all wolves, then, appears consistent with predictions that philopatry will characterize low-fecundity vertebrates in general, as a proximate mechanism that helps generate optimal levels of inbreeding (Shields 1982). As Theberge notes, the wide genetic variability and the relatively great number of named wolf subspecies is more consistent with the view that wolves, by nature, are inbreeding in small demes than with the notion (e.g. Bush 1975) that they are ever highly vagile. The philopatry and social intolerance actually characterizing wolves appear to provide few, if any, opportunities for successful long-distance dispersal, at least under natural conditions (Fritts and Mech 1981).

Wright (1931, 1977) in his classic works first suggested that it was just such a fragmented population structure that would maximize a species' evolutionary potential (see also Franklin 1980, p. 146 and Soule 1980, p. 166). Natural or artificial panmixia (via forced gene flow) are *not* conducive to evolutionary advance or rapid response to changed or changing environments. It is the subdivision that results from inbreeding in small semi-isolated demes that best generates and maintains significant species-wide variability as a hedge against environmental flux. However, this is not necessarily the adaptive function of inbreeding, which may be favoured owing to its conservative effects within demes (Shields 1982). As Theberge notes it is also this subdivision that permits and promotes the generation of locally adapted demes (Baker and Marler 1980), which may be a necessity in normally heterogeneous environments.

4. Risk of reduced genetic variability

Theberge's second theme cautions us about how short-sighted wolf management may increase the level of inbreeding, i.e. reduce N_e, enough to cause significant and detrimental reductions in the species' genetic variability as well as increased inbreeding depression. The genetic variance of a species (megapopulation) can be divided into that occurring: 1) among demes (species-wide polymorphism); 2) among individuals within demes (population polymorphism); and 3) among alleles within individuals (individual heterozygosity). The theoretical reduction in variability associated with inbreeding in smaller populations assumes allelic neutrality, i.e. that natural selection does not discriminate among alternative genotypes and alleles and so does not counteract the effects of drift (Crow and Kimura 1970; Wright 1977, 1978).

If we accept this assumption, then inbreeding will not deplete a widespread species' total genetic variance and so reduce its evolutionary potential. If a fairly large ($N > 1000$) megapopulation is subdivided into small (even $N_e < 50$), partially, or even totally isolated demes, random inbreeding will result in drift and will reduce the within-individual and within-deme components of variation. Individuals will tend to homozygosity and demes to fixation of single alleles at all loci, apparently reducing variability. The genetic variance of the entire species, however, will be maintained as different demes will fix different alternative alleles at frequencies identical with the initial allele frequencies of the megapopulation (Crow and Kimura 1970; Wright 1969, 1977). In a fairly widespread and numerous species like the wolf, subdivision will not reduce species variability, but will redistribute it, as any losses in individual or demic variability will be compensated by equivalent gains in among-deme variability. In nature, irreversible losses of genetic variants and reduced evolutionary potential are only expected in truly rare or endangered species whose megapopulation is small enough to be coincident with a single deme. In addition, as Theberge suggests, if alleles are neutral, and there are many demes, then very low levels of inter-deme migration (even one or two migrants per generation, whether natural or effected artificially) can regenerate or maintain high levels of individual and demic variability, even in the face of considerable inbreeding (Franklin 1980, p. 146; Shields 1982).

Following Franklin (1980) and Soule (1980), Theberge emphasizes the dangers of inbreeding depression as well as drift despite the logical incompatibility of the two. In contrast to the neutrality necessary for drift, inbreeding depression assumes that natural selection does discriminate among alternative alleles, genotypes, or both. Inbreeding is expected to depress fitness by generating less favourable phenotypes more frequently than outbreeding by, first, unmasking deleterious recessives; second, reducing heterozygosity, itself beneficial owing to some form of heterotic selection; or third, both (Franklin 1980, Soule 1980, Crow and Kimura 1970).

The problem of unmasking deleterious recessives is most serious when a normally outbreeding (random mating in large populations) species, which masks and thus accumulates such recessives, is then forced to inbreed (Lerner 1954). It is almost universally acknowledged that normal inbreeders do not accumulate such recessives, because they generate the homozygotes subject to selection more quickly and more often than outbreeders (Franklin 1980, Soule 1980). Thus a normally inbreeding species is expected to suffer little inbreeding depression on theoretical grounds, an inference amply confirmed by data from a variety of inbred species (Soule 1980, p. 158; Shields 1982). As wolves, and many other large or volant vertebrates, appear to be inbreeding consistently in relatively small and semi-isolated demes in nature, e.g. deer (Smith 1979) and the Great Tit (*Parus major*, Van Noordwijk and Scharloo 1981), they are not expected to suffer greatly from the unmasking of deleterious recessives. In addition, if any form of heterotic selection is occurring, it can maintain relatively high levels of individual heterozygosity and demic variability even in the face of significant inbreeding and in the absence of gene flow (Wright 1969, 1977). Soule's (1980, Table 1 and p. 156) list of inbreeding species (including selfing plants) that are more variable than the neutral drift theories would illustrate that the maintenance of relatively high levels of individual and population variability in the face of intense inbreeding is not just a theoretical possibility. Shields (1982) reviews consequences of inbreeding in detail.

5. Conclusions and management implications

Theberge and others (Ralls *et al.* 1979) appear to concur with Soule's (1980, p. 158) assertion that, "it is obvious that conservationists ought to view inbreeding as anathema". On the basis of their dispersal and social behaviour in nature, it appears that wolves may prefer to inbreed in relatively small and semi-isolated demes (for similar conclusions about a variety of mobile vertebrates, see Wright 1977, 1978; Baker and Marler 1980; Shields 1982). For wolves, however, inbreeding does not appear to be an anathema, but rather an adaptive mode of reproduction in their natural environment. This is not meant to imply that extreme inbreeding intensities are never maladaptive; Theberge and others are certainly correct in cautioning about its dangers. However, given sufficient heterosis or frequency-dependent selection, or even neutrality with minimal levels of gene flow, even intensely inbred organisms can maintain individual heterozygosity and demic variability. Even in the absence of gene flow and selection, a fairly widespread species, subdivided into many small and isolated inbred demes, will still maintain species-wide variability despite high levels of genetic drift, which result in decreased individual and within-deme variability. Thus there is little reason to suppose that inbreeding will necessarily result in the depression of a species' evolutionary potential. There are, in fact, reasons for suspecting just the opposite (Wright 1931, 1977).

Although inbreeding depression is a fact of life in many domesticated laboratory plant and animal populations, it has been less evident in natural populations of reputedly outbreeding vertebrates. On closer inspection many of these latter, like the wolf, are actually found to be relatively inbred. Inbreeding is likely to entail a cost in increased segregational loads, but it may also generate significant benefit by maintaining co-adapted complexes of alleles that would be disrupted by wider outbreeding (Shields 1982). That even mild outbreeding can cause a measurable fitness depression (a recombinational load) has been demonstrated both in theory (Williams 1975, Maynard Smith 1978) and in nature, for example in the Great Tit (Van Noordwijk and Scharloo 1981). There is even evidence that sexual imprinting may operate on an "optimal discrepancy" principle, which helps ensure the optimal levels of inbreeding (Bateson 1978, 1979). Finally, I would note here that, *contra* Theberge's assertion, I have suggested that adaptations promoting a specific level of inbreeding, philopatric dispersal or sexual or social imprinting with their resultant aversions or preferences, will only evolve when benefits exceed costs. The fact that the costs are often obvious while the benefits may be more difficult to demonstrate may confuse this issue.

Neither the theoretical implications of an inbreeding optimum nor the fact that wolves appear to be relatively inbred obviate all of Theberge's suggestions for wolf management. It is certainly true that the larger the "managed" area, the larger the megapopulation and, therefore, the healthier the wolf population. In addition, even with a relatively intense inbreeding optimum, there may be cases where artifical gene flow could benefit the wolf, either generally or in specific instances. If environmental conditions were to degenerate to the point where megapopulations decreased in size and became more isolated or were extirpated, then transplants might alleviate the demographic and genetic problems associated with small populations or empty but suitable habitat.

Many who warn of the dangers of inbreeding (Theberge, this publication; Soule 1980; Ralls *et al.* 1979; Senner 1980) might be, and have been, interpreted as suggesting that transplanted individuals be selected indiscriminately, or consciously chosen from among unrelated or distantly related individuals, so that the infusion of new genes is maximal. In the context of optimal inbreeding, it might be more effective to mimic the balance observed in nature more closely. In the case of the wolf, the transfer of a small number of closely related individuals, i.e. among transfers and with the target population (probably by choosing transplants from the nearest viable or flourishing demes), might provide maximum benefits.

By transferring extant packs, or at least breeding pairs, the social and genetic compatibility of the transfers themselves would be assured. Such transfers would be more likely to reproduce in the new area, before any opportunities for gene flow occurred. This would permit an initial environmental screening of their adaptations, or lack thereof, to local selective conditions, before the target gene pool could be affected and perhaps disrupted by any gene flow. The probability of such disruption would be minimized, but not eliminated, by choosing the transfers from nearby areas. Once successful reproduction was established, population pressures and the natural dispersal of the resulting progeny would generate the beneficial demographic or genetic consequences useful for the manager.

The less disruptive form of gene flow engendered by such a program would be less likely to swamp the ecological and genetic coadaptations of both target and transfer populations, and more likely to generate novel hybrid genomes that would be intrinsically coadapted and compatible with local environmental conditions, than would a less balanced approach. It would generate three distinct and potentially competing genomes: the target population; the transfer population; and a subset of their hybrids. Natural selection could then determine which of the three would be more likely to maintain a healthy wolf population in the target area.

In contrast, a higher level of enforced gene flow, by the transfer of greater numbers of less related individuals, would reduce these possibilities. Great numbers of migrants (unless they were intrinsically isolated by a behavioural mechanism, such as sexual imprinting on olfactory dialects, that permits or promotes deme assortative mating despite sympatry; Shields 1982) would be likely to generate only a hybrid swarm, so that the potentially greater value of either parental stock (especially the transfers from a flourishing population) in the target area could not be assessed by manager or natural selection. Similarly, if the transfers were too unrelated, either among themselves or to the target group, the likely effect on hybridization would be significant outbreeding depression and the consequent loss of any opportunity for beneficial gene flow, and a higher probability of the resulting deme showing reduced viability (Shields 1982).

My conclusion is more cautionary than conclusive. Although genetic and evolutionary considerations are likely to be useful, if not necessary, components of the wise management of any vertebrate species, evolutionary theory is not monolithic with respect to its management implications. More data are likely to be required before a truly robust theory of conservation biology can be developed.

Wolf howling in parks — the Algonquin experience in interpretation

Dan Strickland

1. Abstract

This paper reviews the development of "wolf howling" as a means of locating wolves for research purposes in Algonquin Park, Ontario. It also describes the technique's subsequent use for interpretation, with attention to the logistics of leading large numbers of vehicles and people out to hear wolves. From 1963 to 1980, 40 "public wolf howls" were held in the Park. A total of 38 477 people (mean attendance 962) attended. Responses were obtained from wolves on 55% of the attempts. Such events are highly effective as a means of introducing large numbers of people to wolves and have contributed directly and indirectly (through extensive media coverage of the program) to a better public image of the wolf.

2. Introduction

The purpose of this paper is to describe the use of "wolf howling" — that is, the stimulation of wolves into howling through imitations of howls — as a technique for acquainting large numbers of people with wild wolves in park interpretive programs, and its use in Algonquin Provincial Park in particular.

The technique developed as an offshoot from its initial use as a means of locating wolves for research purposes in the late 1950s and early 1960s. The presence of a Wildlife Research Station and substantial wolf population in the large and reasonably pristine area of Algonquin Provincial Park had led the Ontario government to choose the park as the study area for a wolf research program headed by the late Dr. Doug Pimlott. The study (Pimlott *et al.* 1969) sought to elucidate the distribution, movements, breeding biology, food habits, and impact on prey species of wolves within Algonquin.

In an attempt to solve the problem of detecting wolves in a forested environment during summer, Pimlott (unpubl. interview, 11 Jan. 1979, Algonquin Park Museum archives) took up the suggestion by Yorke Edwards, now director of the Provincial Museum in Victoria, BC, of using recorded wolf howls. W.W.H. Gunn, the noted recorder of bird songs, was enlisted to make a recording of the captive wolves, coyotes, and coyote–dog hybrids at the Wildlife Research Station. In August 1959, on the very first attempt made with this recording, replies were obtained from wild wolves. The subsequent development of the technique, using both recordings and human imitations, was documented by Pimlott (1960, unpubl. report of a paper presented to 22nd Midwest Fish and Wildlife Conf., Toronto) and Pimlott *et al.* (1969). It was eventually used to study not only the summer movements and habits of wolves (Joslin 1967, Voigt 1973, Carbyn 1975*a*) but also the biological significance of howling itself (Theberge and Falls 1967).

Other people had already realised that human howls could induce canids to reply. Tolstoy refers to it in his 1862 classic "The Cossacks", and on a recent trip to the Australian outback residents told me that its effectiveness with dingoes (*Canis dingo*) is "common knowledge".

The interpretive use of wolf howling in Algonquin was made possible by the large number of campers (about 100 000 annually) in the organized campgrounds along Highway 60, which passes through the southwest corner of the park for 55 km. Several lectures on wolves by Pimlott had attracted standing-room-only audiences and there was evident interest by many campers who had heard wolves (or researchers) howling in the park. Nevertheless, when the Algonquin Park newsletter, The Raven, invited campers to participate in "an evening of wolf listening" on 17 August 1963, no one on the park staff seriously imagined that many people would turn out. In fact, the response was overwhelming. When a few of the staff casually went down to the appointed meeting place, they found a traffic jam of 180 vehicles and 600 people. Somehow the jumble was sorted out and history's first "public wolf howl" got underway. Surprisingly, given the lack of planning, that first expedition was marginally successful in that it stimulated a faint reply from one wolf. But success was almost irrelevant insofar as all doubts were removed about how great was the level of public interest. The wolf howl organizers also learned they could expect an astonishing degree of patience and co-operation from the participants — such is their almost obsessive desire not to jeopardize their chances of hearing wolves.

In spite of these initial indications, public wolf howls did not immediately become an integral part of the Algonquin interpretive program. Howls were held in 1964 and 1965 but the organizational problems were intimidating and there was poor success in getting answers, partly because of little or no prior searching and partly because the wolf population adjacent to Highway 60 was largely eliminated in the phase of the wolf research program that sought to determine the sex and age structure of the study population. In fact, no wolf howls were held in 1966–68 and it was only in 1969 that they were started again and have continued, basically without interruption, up to the present.

There are two categories of Algonquin wolf howls. Special group wolf howls are unpublicized outings arranged at the request of special groups (generally school groups, naturalist clubs, or side trips from scientific conferences). Groups usually contain 20–60 people and are normally handled by one or two of our naturalist staff. Typically, we have about 5 such groups each year and we estimate that we have looked after about 65 of them (a total of approximately 1700 participants) since the early 1970s.

However, special group wolf howls are minor when compared to the second category, the public wolf howls, which have attracted widespread attention in North America and have introduced thousands of people to the wolf for the first and only time in their lives. Up to and including the 1980 season, we held 40 public wolf howls in Algonquin with a total attendance of 38 477 (an average of 962). Wolves were heard on 55% of the outings.

There are two important observations that can be made about the attendance figures. First, without the public wolf howls, few of those 38 477 people would have heard a wolf, even though they were camped in a park renowned for them. Secondly, we also run regular illustrated evening programs on wolves (without the prospect of hearing the real thing) but these — even with better advance publicity than for public wolf howls — have an average attendance of only 332, only a third of an average wolf howl audience. In other words, the remarkable popularity of public wolf howls can be attributed to an extraordinary desire by people for their own, first-hand contact with wolves.

We have no doubt that wolf howls are the most dramatic way of introducing large numbers of people to wolves and, thanks to the introductory slide talk that is an integral part of each expedition, they are highly effective in placing the experience in the context of wolf ecology.

In Algonquin we have interpretive events, including evening programs, every night of the week but we have adopted the policy of staging public wolf howls no more frequently than once every 7 days. Important as they are, wolves are only one aspect of Algonquin Park and we do not want our interpretive program to dwell on them to the exclusion of all else. For a variety of logistical reasons (such as scheduling days off) we find it necessary to designate one day (traditionally Thursday) as a *possible* public wolf howl day but we actually schedule one only if we have heard wolves the night before at a suitable location, often a rendezvous site. This is for several reasons: with a group of perhaps 1000 people it is impracticable to make more than one or two stops and therefore we cannot search for wolves during the expedition; it avoids raising false hopes in the wolf howl participants; and it reduces unproductive effort and expense. This means, however, that in a given year we may have no public wolf howls at all or perhaps as many as five. It also means that we never announce a public wolf howl until the morning of the day it takes place. This is frustrating to people who want to plan their visits ahead but saves personnel from committing themselves to wolf howls that would almost certainly be unsuccessful.

It is apparent, therefore, that the first step in holding a public wolf howl is to look for wolves. To do this, we schedule two teams of wolf howlers (each consisting of two summer naturalists) to go out on Tuesday and Wednesday nights, starting in the last week of July and continuing if need be until the last week of August. Between them, the two teams cover the park's approximately 80 km of public highway and associated secondary roads. They howl at every suitable location and are out for 3–4 h. We reduce our effort to the level of periodic checking if we find a suitable pack in a rendezvous site but resume full-scale searching if the pack moves.

Assuming we do hear a pack with pups in a suitable location on a Wednesday night, we start preparations for the actual event the following morning. One of the first steps is to put up previously prepared posters at all campground offices, washrooms, lodges, etc., which takes two people with vehicles, working separately, the whole morning. Typically, the phone is also very busy because in the days and weeks leading up to wolf howling season, we have advised people to call us on Thursdays to see if we are going ahead with a wolf howl the same day. Other preparations include arranging for the four to six radio-equipped vehicles that will be required, planning the exact movements and duties of each of the 12–16 staff who will be involved, and the typing and printing of the resulting two-page "battle plan". It may also be necessary to inspect the howling site to take measurements, occasionally to do minor road work, and to decide the optimum placement of the vehicles when the wolf howl actually takes place. All these details are equivalent to a day's work for at least one person.

An hour and a half before the scheduled start of the wolf howl, all participating staff assemble in the Park Museum. We go over the whole operation, make sure everyone understands his role in the exercise, and distribute equipment such as walkie-talkies, traffic safety vests, and flashlights (the kind used by airport ground crews).

At the Outdoor Theatre the staff have various tasks, including counting and directing cars, and efficiently distributing the rush of vehicles so that as many as possible can park simultaneously, thus avoiding a traffic jam on the highway. We must also be prepared to turn people away when the lot is full (approximately 370 vehicles — roughly 1500 people). On one occasion in 1971 we had to turn away 1000 disappointed campers.

After a formal welcome to the wolf howl, a staff member gives an illustrated talk lasting about 30 minutes on Algonquin wolves — their life history, ecology, management, history — and on the research program and the development of wolf howling. The talk includes a short film clip of a wolf howling and a tape recording of a pack of wolves responding to human howls. We do not, of course, guarantee that people are going to hear the real thing later in the evening, but we do tell them that we are going to try at a place where wolves were heard the night before. We end the Outdoor Theatre part of the program by telling people a little about the searching and other preparations that have made the expedition possible. We also give them the instructions to be followed if success is to be achieved and we ask our human howlers to demonstrate the single and group howls that they will use later on. All instructions and information must be given at the Outdoor Theatre because it is impossible to speak to the group at the howling location.

Going down the road to howl for wolves seems simple but in fact many complex details have to be considered for an event of this magnitude to run smoothly and safely.

Some of the more important aspects regarding logistics are as follows:

1. The fastest possible start-up time for a line of 250 cars (i.e. 1000 people) is about 20 minutes. That is, the last car will begin to move 20 minutes after the first one has left. It would be far worse, however, if the drivers had not been asked to back into their initial parking places.
2. It is essential that staff be on hand to direct traffic at every turn throughout the route to be followed. Although drivers have all been instructed to follow the car in front of them, gaps sometimes develop and without adequate direction many drivers might lose their way. The traffic controllers must be able to leave their specific locations when their work is finished. This means there must be space in a vehicle to deliver them and pick them up.
3. A line of 250 vehicles, even when moving at only 50 km/h, still stretches for at least 10 km. As no one driver can see everything that is going on, radio communication between the head and tail of the line, and other key positions, is essential.

Wolf howling is readily elicited by human howls and this was effectively carried out for interpretive programs in Algonquin Provincial Park, Ontario (photo: Scot Stewart)

4. For convenience it is important that the long line of vehicles comes to a halt centred on the wolf howl location. Knowing the number of vehicles and the length they occupy when parked (about 0.7 km per 100 vehicles) we can calculate where the lead vehicle should be halted. Usually we split the line of vehicles in two and turn the leading group around at some convenient point, thereby centring both groups on the howl location.
5. When the wolf howl is being held on a road open to other members of the public, official vehicles must be stationed beyond each end of the line of parked cars to intercept through traffic, and either to halt it while an attempt is being made to howl up the wolves, or advise it to proceed (with caution) before we try to call the wolves.

Carrying out a public wolf howl may seem more like an exercise in traffic control than engaging in a wildlife experience. In fact, despite the presence of perhaps 1000 people and 250 cars, the howls are a huge success; indeed the procession of cars through the dark Algonquin night evidently heightens the excitement of the occasion. The patience of the participants, waiting in silence for the last arrivals, is testimony to the longing of urban man for the natural environment.

On those occasions when the human howls are answered by a chorus of wolves from somewhere in the surrounding wilderness, the impact on participants is profound and, I think, lasting. No other interpretive event in my experience is so effective in conveying the concept of wildlife and its place in the natural system.

It is interesting to view public wolf howls in the context of evolving attitudes toward the wolf. In the early days of Algonquin Park it was taken for granted that the destruction of wolves was a normal and desirable pursuit. George Bartlett, Algonquin Park Superintendent from 1898 to 1922, regularly wrote articles for Rod and Gun magazine with such titles as "How shall we destroy the wolf?" (Bartlett 1909). Apparently the only controversy in those days was whether the use of poison was legitimate.

The next step in the evolution of the Ontario government's attitude toward wolves was the commencement of the Algonquin wolf research program and the concomitant protection of wolves in the park. Even so, the program ended in 1964 and 1965 with a determined effort to collect most of the wolves in the Park study area. Less than a decade later, even this sort of destruction of wolves had become unthinkable. For in that period the public image of the wolf had been transformed from a mysterious fearsome beast to the very symbol of the wild country people come to enjoy in Algonquin. Many factors are responsible for this decided shift in public attitudes but we believe that the interpretive use of wolf howling has made a significant contribution. To our knowledge there have been at least 18 articles on the Algonquin program in the popular press of North America. There have also been radio and television programs featuring the wolf howls. Letters of enquiry regularly come to us from all over North America and occasionally from Europe.

Wolf howling programs of various kinds have been instituted in Prince Albert, Riding Mountain, and Jasper National Parks and in Sibley Provincial Park in Ontario. So far, these have been conducted on a much smaller scale than those in Algonquin but they have met with the same extraordinarily enthusiastic response from the public. In a very real sense, it can be said that wolves now regularly meet and, through their own howls, convince thousands of park visitors that they have a place in our world.

Wolf management and harvest patterns on the Kenai National Wildlife Refuge, Alaska*

Rolf O. Peterson
Theodore N. Bailey
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1. Abstract

Legislation enacted in 1980 by the US Congress broadly defined management objectives for the newly established Kenai National Wildlife Refuge (KNWR), formerly the Kenai National Moose Range, and ordered that a comprehensive planning effort be undertaken for the Refuge. Because wolves are prominent carnivores that have been hunted in the KNWR only since 1974, wolf harvest characteristics are germane to planning efforts by the US Fish and Wildlife Service (USF&WS) and the Alaska Department of Fish and Game (ADF&G). Wolf harvest on the KNWR increased steadily between the first trophy hunting season in 1974/75 and the 1979/80 hunting and trapping season. Although "land-and-shoot" harvest of wolves has sporadically been high on the KNWR, the principal method used appears to be snaring. The proportion of radio-collared wolves harvested on a study area on the northern half of the KNWR increased between 1976 and 1981; 39% of those available were killed in 1980/81. Preliminary analysis of data from the study area suggests that harvests by humans exceeding 25% of the early winter wolf population would produce a decline in numbers the following year; harvests of this magnitude occurred on the study area in 1979/80 and 1980/81. Wolf management objectives and actions by USF&WS and ADF&G are reviewed and a suggestion made that wolf management be incorporated into inter-agency planning efforts and integrated with management of habitat and other species in this ecosystem.

2. Introduction

The Kenai Peninsula, a 26 000 km^2 land mass connected by a narrow isthmus to the mainland in south-central Alaska, has been famous for decades as a major area for trophy hunting of big game. Moose (*Alces alces*) are prominent in the natural history of the region. The area has seen intensive human use since the Kenai gold rush in 1895 and 1896 (Peterson and Woolington 1982), and continues to receive heavy recreational use, including hunting and trapping, because of its close proximity to half of Alaska's human population.

The Kenai National Wildlife Refuge (KNWR), formerly Kenai National Moose Range, covers 6910 km^2 on the western half of the peninsula. In 1976 the US Fish and Wildlife Service (USF&WS), which is responsible for managing the refuge, and the Alaska Department of Fish and Game (ADF&G) initiated a co-operative predator–prey study of wolves (*Canis lupus*), bears (primarily *Ursus americanus*), and moose. Studies of wolf ecology and wolf–moose relationships were conducted from 1976 to the present. Our study area on the northern half of the KNWR covered approximately 3700 km^2. In the late 1970s this region supported about 1 moose/km^2 and 1 wolf/60 km^2 (Bailey 1978, Peterson and Woolington 1982).

Human use early in this century had a great effect on many wildlife species on the Kenai Peninsula. Commercial hunting and a general disregard for the minimal game laws that existed led to reductions in moose and Dall sheep (*Ovis dalli*) populations (Studley 1912) and disappearance of caribou (*Rangifer tarandus granti*) (Davis and Franzmann 1979). There are many references to the widespread use of poison to reduce carnivores; this was considered instrumental in the elimination of wolves from this large land mass by about 1915 (Peterson and Woolington 1982). Moose, on the other hand, eventually benefited from extensive fires that occurred during the gold mining era and populations reached high densities in parts of the western Kenai Peninsula by the 1920s.

The significance of the low-lying western half of the peninsula as moose habitat was widely recognized by the 1920s and 1930s. This factor, together with concern for Dall sheep in the adjacent mountains, led to the creation of the Kenai National Moose Range by Executive Order of the President in 1941... "for the purpose of protecting the natural breeding and feeding range of the giant Kenai moose..." (Bailey 1978). A 1250 km^2 fire in 1947 created optimum moose habitat and led to peak moose populations in this area in the 1950s and early 1960s (LeResche *et al.* 1974). However, in the early 1970s a series of severe winters, together with declining habitat, reduced moose on the KNWR to approximately their pre-1947 burn density (Oldemeyer *et al.* 1977, Bailey and Bangs 1980).

From 1915 to about 1960 there was no evidence of a reproducing wolf population anywhere on the Kenai Peninsula, and for some of this period wolf populations on the adjacent mainland were locally reduced by federal wolf control programs (Peterson and Woolington 1982). Reports of single wolves in the late 1950s and the sighting of one wolf by an ADF&G biologist in 1961 led to the closure of the Kenai Peninsula to all taking of wolves, a restriction that remained in effect until 1974.

In this paper we shall review Kenai wolf management and harvest patterns since 1974, especially on the KNWR. Management objectives of such agencies as ADF&G and USF&WS will be discussed. We hope this will provide background and a common basis for future discussion of Kenai wolf management, an undoubtedly controversial issue. Where applicable, we shall provide pertinent data and conclusions resulting from our recent wolf research on the KNWR (Peterson and Woolington 1982).

3. Wildlife administration relating to wolves

Since 1960, management of resident wildlife has been the responsibility of the State of Alaska, with regulations set by the Alaska Board of Game, appointed by the Governor. The Board acts annually on recommendations received from the ADF&G, USF&WS, special interest groups, and the general public. Hunting seasons and bag limits for hunters and trappers usually follow closely the recommendations of the ADF&G. Because the USF&WS regulates access and uses of Refuge lands, it can issue more restrictive special regulations affecting hunting and trapping on Refuges.[1]

[1] The court decisions regarding Federal/State jurisdiction over wolves and other resident wildlife (see Harbo and Dean, this publication) were not intended to apply to National Parks and National Wildlife Refuges, many of which have specific Congressionally mandated objectives for resident wildlife species, as stated in the 1980 Alaska National Interest Lands and Conservation Act.

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In preliminary wildlife management plans issued by ADF&G in 1976, the recreational potential of wolf harvests on the Kenai was stressed. The Kenai Peninsula was the only large area in Alaska where the primary objective was to "provide the greatest opportunity to participate in hunting and trapping of wolves", an objective that emphasizes the recreational value of this wolf population rather than the sustaining of a maximum yield of wolves. The main objective for most of Alaska is "optimum harvest", which "emphasizes the yield of animals for human use", including both predator and prey. In some areas of Alaska wolf control measures have been considered necessary in order to maintain or increase harvestable prey populations (Harbo and Dean, this publication). Presumably, recreational harvest of wolves would control short-term wolf increases and reduce potential management problems caused by peak wolf populations. ADF&G and the Board of Game both consider wolf control to be a valid management action in specific instances to promote increases in game populations, but intentional wolf control is limited to cases where "substantial data" justify the action and "only after it has been shown that public hunting and trapping harvests will not achieve the stated management goals" (Preliminary Wildlife Management Plan 1976, ADF&G).

The Management Plan states that as the hunting of wolves increases on the Kenai, reduced seasons and bag limits might be necessary to reduce wolf harvests. The only management change implemented by the Board since 1976, however, was an increase from two to four wolves in the bag limit for hunters, in accordance with recommendations (Spraker 1980, Fed. Aid Wildl. Res. Rep.) to reduce wolf populations and thus, presumably, loss of moose by predation.

The only USF&WS management objectives specifically stated for wolves were contained in Environmental Impact Assessments written in 1974 and 1976 (KNWR files), preceding the opening of the KNWR to hunting and trapping of wolves; the stated intent of the USF&WS was that human harvest of wolves should not exceed the level that could be annually replaced. Objectives for the Kenai Refuge were recently re-defined by the Alaska National Interest Lands Conservation Act[1] of 1980. One of the diverse aims of the KNWR is "to conserve fish and wildlife populations and habitats in their natural diversity including, but not limited to, moose, bears, mountain goats, Dall sheep, wolves and other furbearers. . ." The Congress charged the USF&WS with the responsibility for developing and implementing a Comprehensive Conservation Plan for new refuges, and the Kenai Refuge will be the first to undertake the planning effort.

New management directions for the KNWR will follow the general philosophy outlined in the Congressional legislation that established the Refuge. Key concepts implicit in enabling legislation, and recent directions in refuge management, include preservation of the ecosystem by maintaining a natural diversity of wildlife species, decreased emphasis on game production, public use consistent with long-term maintenance of the above values, and high quality hunting and trapping programs.

4. Kenai wolf research highlights

Wolf research over the past 5 years has revealed many characteristics of the wolf population and its interaction with Kenai moose; detailed results are to be published elsewhere. The 1976 wolf density in the Kenai study area on the northern half of the KNWR was relatively high for Alaska, at 1 wolf/60 km^2, but not high in relation to prey biomass (1 wolf/55 moose in midwinter). Peterson and Woolington (1982) proposed that the wolf population was at or near natural saturation density in 1976. On the study area, packs were initially large, with an average early winter size of 12 wolves, but by 1980 had declined to about 6 wolves as harvesting by man increased. The proportion of pups in the wolf packs studied increased because average pack size was smaller, but there was little evidence of increased pup recruitment per pack to compensate for increased mortality.

[1]Major federal legislation that formally established various large tracts of "national interest" lands to be managed by the US National Park Service and the US Fish and Wildl. Serv.

Predation rates for Kenai wolf packs in winter were intermediate in the range of kill rates observed elsewhere. Wolves killed calves and adult moose (almost exclusively old cow moose) in winter and probably relied heavily on calves in summer (Peterson *et al.*, in prep.). There were no abundant alternative prey species. An estimated 8% of the adult moose on the study area and an average of 13% of calves in their first year of life were killed by wolves annually (Peterson *et al.*, in prep.).

Over a third of the calves killed were in poor condition, with a bone marrow fat content of less than 10%. Concurrent studies by Franzmann *et al.* (1980) indicated significant predation on young calves by black bears, accounting for 40% loss of calves on a study area that was burned in 1947. Peterson and Woolington (1982) suggested that in view of the marginal habitat available to moose on most of the study area (with the exception of 350 km^2 burned in 1969) the moose population had relatively little growth potential even if wolf predation could be reduced.

Hunter harvest of moose on the study area declined from a peak of about 1100 moose in 1971, when cow-moose hunting was allowed, to about 250 in the late 1970s (Spraker 1980, Fed. Aid Wildl. Res. Rep.). Hunting pressure on moose (bulls only) continues to be high and is largely responsible for a highly skewed adult sex ratio of 15 bulls/100 cows on the northern portion of the KNWR.

5. Characteristics of Kenai wolf harvest

During the period of total protection, the Kenai wolf population became rapidly re-established, and large packs were reported from all major areas of the Refuge by the early 1970s. Following 3 years of discussion between the ADF&G and the USF&WS, a trophy hunting season was approved by both parties in 1974, permitting a 4-month hunting season with a limit of 1 wolf/hunter. In 1975 the Board approved the addition of a 5-month trapping season with no limit — the same trapping regulations that applied elsewhere in Alaska — but because the accuracy of wolf population estimates was in question, the USF&WS closed half of the KNWR to wolf trapping. In 1976, however, concurrent with the initiation of a predator–prey study sponsored jointly by ADF&G and USF&WS, both wolf hunting and trapping were allowed over the entire KNWR except for the surfaces of two large lakes, which were kept closed in order to prevent trappers with aircraft from taking wolves by using a land-and-shoot technique. Since 1978 there have been no additional federal special regulations affecting wolf harvest on the KNWR except for a short-lived closure in 1979 designed to limit land-and-shoot harvest of furbearers. The sporadic special regulations issued previously by the USF&WS reflect an attempt to control increasing wolf harvests on the KNWR. ADF&G recommendations (Spraker 1980, Fed. Aid Wildl. Res. Rep.), on the other hand, have called for increased wolf harvests in the belief that the moose population would benefit.

Mortality data for radio-collared wolves (Table 1) reveal that few wolves die of causes unrelated to harvest by man, with 88% of all mortality recorded after the age of 6 months attributable to human causes. Radio-collared wolves lived an average of 16 months after being collared. Wolves most vulnerable to human harvest were dispersing young adults, which had a mortality rate of at least 42%. The average period between dispersal and death was 5 months.

The sample of radio-collared wolves provided a different picture of the methods used to harvest wolves than did the mandatory ADF&G reporting forms (Table 2). We tried to contact personally every individual who killed a radio-collared wolf, and discussed the circumstances of each kill. Table 2 shows that most harvested radio-collared wolves were either shot or snared, and only one (3%) was known to have been trapped. We suggest that the distinction between snaring and trapping may not be reported accurately by individuals registering wolf hides. Snaring seems to be the principal method of harvesting Kenai wolves, because wolves recorded as being shot included those taken both by land-and-shoot trappers and by ground-based hunters acting opportunistically.

Table 1
Cause of death of radio-collared wolves on the KNWR study area, 1976–80

Cause of mortality	Method	*N*
Human	Snared	15
	Shot	16
	Trapped	1
	Unknown	1
Natural		3
Total		36

Table 2
Percentages of wolves taken using different methods of harvest on the Kenai Peninsula, Alaska

Source of data	*N*	Method (%) Ground shooting	Trapping	Snaring	Other	Unknown
ADF&G sealed (%)	207	41	32	24	2	1
Radio-collared wolves (%)	35	46	3	49	–	3

There is some misunderstanding about how aircraft may be used in taking wolves in Alaska. The federal Airborne Hunting Act of 1972 forbids shooting of wildlife from aircraft, or herding or harassment of animals with aircraft, except under special permits issued by states for management purposes. ADF&G currently issues aerial hunting permits in several areas where they wish to reduce wolf populations. This is a practice distinct from harvesting by the commonly used technique of land-and-shoot, which is legal under trapping regulations that allow the hunter to spot free-ranging furbearers from an aircraft, but to shoot only after landing. A number of individuals in Alaska are quite proficient at land-and-shoot trapping, and this technique has been used with considerable success by a few individuals on the KNWR. Hunting regulations forbid the shooting of big game on the "same day airborne", but this regulation does not apply to furbearers. Wolves and wolverines (*Gulo luscus*) are classified as both big game and furbearers, and while a licensed hunter must not spot wolves from aircraft and proceed to land and shoot, a licensed trapper can do so legally, with no limit on the number of wolves he may take in this manner.

Table 3
Proportion of aircraft users among "trappers" on the KNWR

Regulatory year	Total no. of permits issued	Aircraft users *N*	%
1976–77	86	12	14
1977–78	86	21	24
1978–79	96	30	31
1979–80*	97rq 32	33	

*As of February 1980.

Use of aircraft in the Kenai area increased dramatically in the mid-1970s (Federal Aviation Administration, pers. comm.) and the proportion of trappers that use aircraft on the KNWR is about one out of three (Table 3). There are at least 1200 small privately owned aircraft within 80 km of the KNWR (FAA records, 1979), mostly in the Anchorage area.

6. Kenai wolf harvest trends

Peninsula-wide wolf harvest reached a peak in 1978/79 after increasing steadily since the first hunting season in 1974/75. The increase in the number of wolves taken on the KNWR was matched by a similar increase in the mortality rates of radio-collared wolves from human harvest (Table 4). In 1980/81, 39% of the radio-collared wolves available during a hunting and trapping season were killed.

Although there have been instances of high harvests of wolves on the Kenai by land-and-shoot trappers, the steady increase in total wolf harvest on the KNWR cannot be attributed to increased use of aircraft. The KNWR exists in virtually a semi-urban situation, with 200 000 people living less than an hour's flight or half-day's drive away. Increased wolf harvest has

Table 4
Wolf harvest summary, Kenai Peninsula

Year	Total wolves taken on Kenai Peninsula	Method*: Ground shooting†	Method*: Trapping	Method*: Snaring	Method*: Other	Method*: Unknown	Total wolves taken on KNWR	Proportion of harvested wolves taken with aircraft, (%)‡	No. of radio-collared wolves taken per year	No. of radio-collared wolves avail. per year	Proportion of radio-collared wolves taken per year (%)	Over winter loss in radio-collared packs (%)
1974–75	6	3	1	0	0	2	1	0	–	–	–	–
1975–76	21	9	8	4	0	0	4	0	–	–	–	–
1976–77	12	7	5	0	0	0	6	0	0	11	0	26
1977–78	36	19	6	10	1	0	13	46	3	25	12	29
1978–79	55	20	22	9	3	1	32	41	9	37	24	43
1979–80	43	11	18	13	1	0	37	14	10	37	27	57
1980–81	34	15	6	13	0	0	17	0	10	26	39	n.a.
Total	207	84	66	49	5	3						

*As recorded on ADF&G sealing forms.
†Including all "land-and-shoot" harvest.
‡Data available for KNWR only.

been associated with increased public awareness of the presence of wolves, to which the research effort itself has contributed to some extent.

7. Impact of harvest on the wolf population

The degree to which a wolf population can compensate for human harvest has been poorly documented. Although there is evidence that some wolf populations can annually replace nearly 50% of total losses (Mech 1970, Peterson and Woolington 1982), the distinction between mortality from human harvest and total over-winter loss is often ignored, leading to the incorrect assertion that wolf populations can universally maintain pre-harvest densities at a *harvest* level of 50% (Preliminary Alaska Wildlife Management Plan 1976, Rearden 1980). From data on Kenai wolves, we estimated that a recorded (reported) harvest of 25% would actually produce an average over-winter loss of 43%, the difference being attributed to natural mortality, dispersal loss, and unreported harvest or human-caused mortality. From an analysis of population age structure, observed mortality, dispersal, and wolf density, we earlier suggested that a recorded human harvest in excess of 25% of the early winter wolf population would reduce density the following year, as annual losses could not be replaced by reproduction. Wolf harvests in 1979/80 and 1980/81 on the study area exceeded 25% of the early winter wolf population; preliminary data suggest that wolf density did subsequently decline. Key characteristics of the Kenai wolf population that might limit the applicability of these figures to other populations are:

1) generally one average-sized litter of pups in each pack each year, regardless of pack size;
2) large pack size, averaging 12 wolves in early winter; for a given litter size, recruitment rate will be higher for small packs than large packs;
3) wolf density originally believed to be close to natural saturation density;
4) unreported over-winter loss of 18% due to natural mortality and dispersal.

Additional empirical evidence that wolf populations often cannot be maintained with 50% overwinter loss is provided by Van Ballenberghe *et al.* (1975), Van Ballenberghe (1981), and Mech (1977*a*). Undoubtedly a review of all available data on the subject and future research will allow us to refine our thinking on the subject of critical levels of overwintering wolf mortality.

8. Concluding remarks

Wolf management on the KNWR will continue to be controversial because of agencies' differing management objectives. Interagency agreement will be facilitated if management objectives are clearly stated and, if possible, jointly proposed. Wolf population responses reflect to a large extent changes in resource levels and characteristics at lower trophic levels, as well as human harvest patterns. It is imperative that wolf management be integrated with management of habitat and prey species, especially moose, and that allowable human harvest be compatible with the long-term goal of preserving natural diversity in this ecosystem.

Wolf-related caribou mortality on a calving ground in north-central Canada

Frank L. Miller

1. Abstract

Mortality of newborn barren-ground caribou was studied 1 June – 29 July 1970. The study was carried out on the calving ground of the Kaminuriak caribou in the south-central District of Keewatin, NWT, by low-level aerial searches. Fifty-seven calf carcasses were found and necropsied. Predation by wolves accounted for 31.6% of the deaths of newborn calves. Other causes of death included abandonment by maternal cows (separation), stillbirths, physiological or pathological disorders, malnutrition, pneumonia, and injuries, in that order of frequency. High loss of caribou calves shortly after birth and throughout the first year of life to wolves is a major limitation to population growth. Thus, the desirability of reducing predation by wolves on caribou calves should be considered by wildlife management agencies.

Several of the large migratory populations of barren-ground caribou (*Rangifer tarandus groenlandicus*) in north-central mainland Canada are experiencing serious declines in numbers (Thomas 1981). Over-harvesting of these caribou has been identified as the primary cause of the declines. Normal wolf predation in addition to current high rates of harvesting could further reduce their numbers. As a result there has been a renewal of interest in the wolf–caribou relationship by people concerned with obtaining sustained annual yields of caribou from these populations.

Wolf predation accounts for a large proportion of the deaths of newborn caribou, especially during calving periods with favourable weather and foraging conditions, when mortality of neonate caribou caused by other factors is negligible. There are few data on the impact of wolves on newborn caribou. Therefore I am presenting findings from our 1970 study of calf mortality on the calving ground of the Kaminuriak caribou (Miller and Broughton 1974) to provide some insight on the subject.[1]

[1] Editor's note: Caribou declines have become a pressing issue in northern Canada. Because no new information on wolf predation was available, Frank Miller submitted this material for publication.

Causes of mortality among newborn calves of the Kaminuriak caribou population were investigated between 1 June and 29 July 1970 (Miller and Broughton 1974). The caribou calve on the open tundra near Kaminuriak Lake in the central District of Keewatin, NWT. We spent 180 hours searching for dead calves, using a Hiller 12-E helicopter at a height of 30–100 m.

Necropsies were carried out on 57 calves and 8 adult female caribou. Causes of mortality to newborn calves were found to be, in descending order of frequency of occurrence: predation by wolves, 31.6%; abandonment by maternal cows, 21.1%; stillbirths, 10.5%; physiological or pathological disorders, 8.8%; pneumonia, 7.0%; malnutrition, 7.0%; and injuries 5.2%. We could not determine the cause of death of five calves (8.8%) as too much postmortem change had occurred before the carcasses were found. Two of the adult cows had been killed by wolves. Three had died from complications during parturition: one of a ruptured uterus, one of peritonitis, and one had not expelled her placenta and was infected with besnoitiosis. We shot two adult cows because they had difficulty moving: one had besnoitiosis and the other reacted positively to brucellosis. We also shot a cow suffering from *Escherichia coli*, which had caused her male calf to die from malnutrition.

Wolves had killed 18 of the calves (8 females, 6 male, and 4 of undetermined sex). Eleven (61%) of these were less than 2 weeks old, and the remaining seven were between 2 and 6 weeks of age. Consumption of the wolf-killed calves ranged from 0 to 90% and averaged 21.7%. We probably missed the remains of most calves that had been more than 80% eaten. Six (33.3%) of the wolf-killed calves were uneaten; seven (38.9%) had part or all of their viscera taken; and five (27.8%) were more heavily utilized.

An interesting aspect of the utilization of caribou calves was the wolves' apparent preference for eating milk curds, then viscera, and finally flesh. It appeared, based on examination of carcasses with only part of the viscera missing, that wolves deliberately opened stomachs of calves and consumed the milk curds. We assume that wolves ate the curds from all the calves they eviscerated, as we did not find any curds around those carcasses. Examination in June 1981 of newborn calves of the Beverly caribou population confirmed that wolves did indeed have a strong preference for milk curds (Miller *et al.*, in press).

Abandonment by or separation from the dam was probably not as prevalent among newborn calves as the 21.1% sample suggests. Nine of the 12 calves listed under death by abandonment were only hours old when they died. In fact they probably died of secondary (premature birth) neonatal atelectasis rather than from malnutrition caused by abandonment or separation. One of the other three calves was several days old and may have died of malnutrition. We shot the remaining two calves because they probably would have died of malnutrition or been victims of predation.

Two of the four calves listed as dying of malnutrition did so because their dams died first. The other two calves may have succumbed for the same reason or they might have been abandoned or separated from their dams (see Miller and Broughton 1974 for more details on the deaths of individual calves).

Eleven of the wolf-killed calves had been bitten in the head: six had punctured and fractured skulls and five had crushed crania. Parts of the cranial bones were often missing. All calves had extensive haemorrhaging on areas of the back or shoulders.

The pattern indicated by minimal carcass utilization, killing by biting the head or neck, and prevalent consumption of viscera closely resembles descriptions by White (1973) of white-tailed deer fawns (*Odocoileus virginianus*) killed by coyotes (*Canis latrans*).

After 1 July all the wolf kills found were in dense stands of willow (*Salix* spp.) or birch (*Betula* spp.), suggesting that the wolves had ambushed the moving caribou. In one instance the same wolf had apparently killed three calves: two lay within 3 m of each other and the third about 35 m away. Henshaw (1968, 1970) noted that caribou were hesitant about crossing through riparian willows and that some

Wolves feeding on an ungulate carcass. Predation rates by wolves show a wide range of frequencies and are largely dependent on the availability of prey (photo: W.C. Mason)

animals were visibly alarmed. He attributed this behaviour to a response to the methods of predation used by wolves and bears.

We found two adult cows that had been killed by wolves. Both seemed to be in good physical condition for the time of year. We estimated (by tooth wear) the age of one to be 8–10 years; it was only about 5% utilized. We estimated (also by tooth wear) that the other female was 4–5 years old; it was about 20% utilized. She had dropped her calf before she was killed but it was not found.

Our examination of the wolf-killed calves, with one exception, gave us no reason to believe that these calves were predisposed to some other form of mortality. The exception was a female over 2 weeks of age with an abscess that had caused the right lobe of the lung to adhere to the diaphragm. None of the wolf-killed calves showed any signs of physiological disorders.

Our observations of caribou groups and especially cow–calf pairs during the calving period gave us no indication that abandonment or separation from the dam was prevalent among newborn calves (although it does occur). Therefore we do not believe that wolves waste time hunting for the relatively few calves unaccompanied by cows; many calves with dams can apparently be taken at will.

The haemorrhagic condition of all carcasses fed on or mauled indicated that the caribou were alive when attacked. There were no active wolf dens on the calving ground. It is unlikely that wolves returned to their kills because they had to keep up with the caribou, who moved continuously after the peak of calving.

Wolves are readily able to kill healthy caribou calves. Therefore there seems to be no reason for them to select weakened or disabled calves. This is particularly true during the calving period and for the first few weeks thereafter. Therefore I suggest that, in general, most wolf predation on newborn caribou calves is not compensatory.

Although 68.4% of the calves in the sample had died from causes other than predation, it is my opinion that this percentage cannot be reduced by any feasible management practices. Results so far indicate that wolves remain the most readily manageable of mortality factors affecting migratory barren-ground caribou, but at the same time their impacts on caribou populations are possibly the least understood (Miller and Broughton 1974).

Humans are in theory the most manageable of agents influencing the caribou but I am excluding them because socio-political considerations related to the control of human harvesters extend beyond the scope of this paper. I think it would be biologically sound to reduce wolf predation on migratory barren-ground caribou populations that are declining in numbers. Maintenance of wolf populations in a manner that would ensure maximum survival of newborn caribou calves would be especially desirable as part of an extensive management plan. High loss of caribou calves shortly after birth and throughout the first year of life to wolves is obviously a major limitation to population growth. Therefore the desirability of reducing predation by wolves on caribou calves should be considered as a valid management tool by concerned wildlife agencies.

Wolf predation of livestock in western Canada

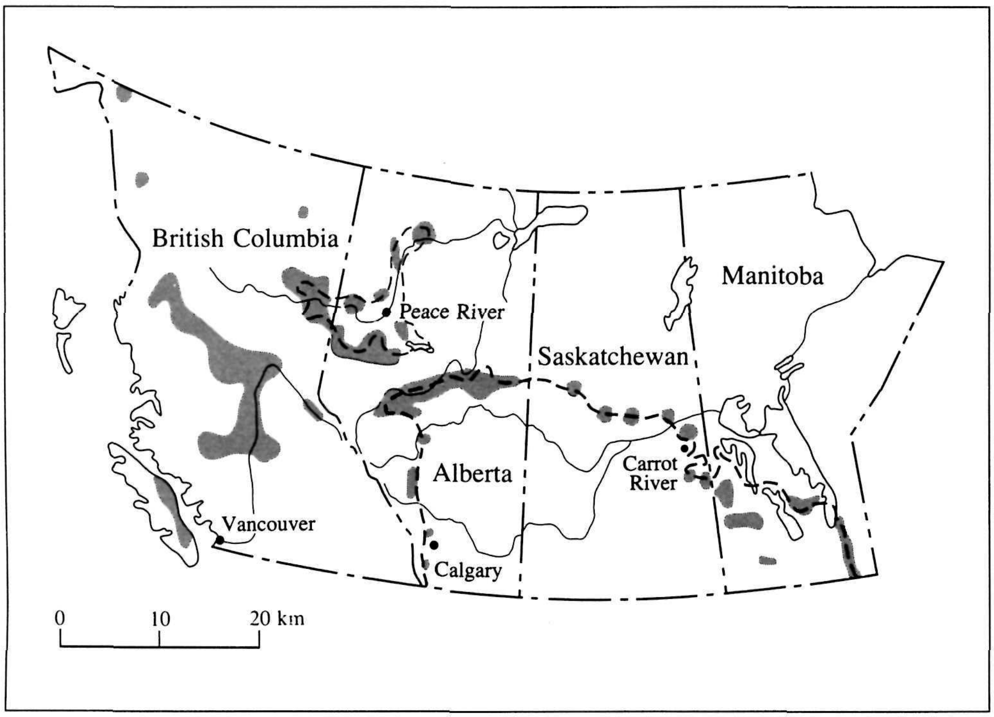
J.R. Gunson

1. Abstract

Variations in the occurrences of wolf depredations of livestock among provinces in western Canada are related to the length of forest–agricultural fringe and the extent of livestock production in forested areas. Depredations occurred most frequently in British Columbia, followed by Alberta; documentation of predation was more complete in these two provinces. Cattle were killed more frequently than other domestic prey — 92% of approved indemnity claims in Alberta and 64% of confirmed kills in BC. Cattle losses to wolves occurred most frequently in late summer and infrequently during the denning period. Wolves selectively killed calves and yearlings rather than cows; calves represented 62 and 66% of cattle losses in Alberta and BC, respectively. Not all complaints were valid wolf kills; 36% of 496 complaints in northwestern Alberta included confirmed kills. Compensation was available to producers only in Alberta, where 384 claims were approved during 1974–80. Wolf control was conducted in all provinces following confirmed predation; both reactive and preventive control measures were utilized. Commercial/recreational trapping of wolves in fringe areas should be encouraged to prevent depredations.

In most of western Canada wolves increased in numbers and extended their range to the south during the late 1930s to early 1950s (Stelfox 1969; Nowak, this publication). During this period agriculture expanded into some northern areas and depredations became more common, although not well documented (Soper 1948). During the 1950s wolves were intensively controlled in western Canada, mostly for the management of big game and rabies (Pimlott 1961), and depredations apparently occurred less frequently. During the 1960s and 1970s governmental wolf control for game management reasons was reduced or eliminated in all four provinces and wolves increased in range and numbers. This paper summarizes wolf–livestock predation in western Canada during the decade prior to 1981.

Figure 1



– – – – Forest-agricultural fringe
Areas with wolf predation on livestock

Figure 1
Locations of the forest–agricultural fringe and areas of wolf–livestock depredations in western Canada

2. Introduction

Wolves (*Canis lupus*) were virtually eliminated from the western USA partly because of their predation of livestock (Young 1944, Seton 1929). In Eurasia, wolf–livestock depredations have occurred in historical and modern times (Bibikov 1975, Haglund 1975, Boitani and Zimen 1975). In western Canada depredations were reported as early as 1841 at Fort Vancouver (Young 1944), in 1857 at Fort Carlton (Spry 1963), in extreme southern Alberta in the late 1870s (Rodney 1969), west of Calgary in 1885 (McCowan 1950), and in southern Manitoba in 1886 (Seton 1929). Following severe reductions in numbers of wolves in most of western Canada during the late 1800s and continuing into the 1930s (Stelfox 1969; J. Robertson 1974, Man. Wildl. Br., unpubl. rep.) livestock depredations were uncommon during the first quarter of this century.

3. Distribution, numbers, and types of depredations

Wolf predation of livestock occurs primarily along the forest–agricultural fringe, which varies considerably in length between provinces (Fig. 1). This fringe is most abrupt in Saskatchewan, surrounds forested islands of wolf habitat in Manitoba, is extensive in Alberta and occurs as sporadic, often isolated valley bottoms and interior grasslands in mountainous BC. Occurrence of depredations in these fringe areas is influenced by the status of wolves, number of livestock, quality of animal husbandry and, potentially, by the relative abundance of native prey.

Numbers of livestock in the respective provinces (Table 1) are not relative indicators of potential wolf depredations because most livestock operations occur in areas without wolves. Rough estimates of the numbers (×1000) of

Table 1
Numbers of livestock (×1000) in western Canada, July 1980

Province	Cattle*	Sheep†	Swine*
Alberta	4250	200	1310
BC	749	60	180
Manitoba	1186	28	823
Saskatchewan	2590	97	640

*Canadian Livestock Feed Board.
†Statistics Canada.

cattle pastured annually in wolf range are Alberta 300, BC 434, Manitoba 172, and Saskatchewan <100.

In Manitoba, depredations on livestock apparently occurred more frequently than in Saskatchewan, but less frequently than in Alberta or BC, although provincial wolf depredation records were not available (R. Stardom, pers. comm.). Annual depredations were reported only from the Interlake area (Stardom, this publication). Carbyn (1980, CWS, unpubl. rep.) noted a report of 17 cattle killed by wolves in this area in 1979. Most depredations in the Interlake area occurred on community pastures and grazing leases. Occasional complaints were also received from the peripheries of Duck Mountain and South Porcupine forests and from the southeast and northwest forest–agricultural fringes of Manitoba.

Carbyn noted four reports on wolf–livestock depredations adjacent to Riding Mountain National Park in 1975 and 1976 during a period when the density of wolves in the park was high. Wolves were taken following two of these complaints, where kills or attacks were confirmed. Carbyn also noted reports of about 20 wolf-killed sheep in southern Manitoba in 1975; a lone wolf was implicated. Based on 1059 questionnaires sent to 10% of cattle producers in potential wolf–livestock problem areas in Manitoba, Hill (1979) recorded eight farmers reporting losses of $2880 during 1973/74.

In Saskatchewan, H. Strom (pers. comm.) reported 11 wolf complaints during 11 years (1969–79) involving 115 cattle, 2 horses, and 5 unspecified livestock units (from correspondence with field staff in 1981, as few, if any, records have been maintained). Strom noted only one area where high numbers of livestock were missing; these losses occurred in 1969 and 1975 on the Smoky Burn Community pasture near Carrot River. W. Runge (pers. comm.) noted that no cases of wolf predation on livestock were reported from either Cumberland Farm or Mile 30 Farm in northeastern Saskatchewan where several hundred head of cattle were annually pastured in areas frequented by wolves.

In Alberta, livestock predations by wolves have been common since 1972; wolves reoccupied most of the forested areas of the province following rabies control during 1952–56 (Gunson, this publication). Occasional depredations were reported during the 1960s. During the 9-year period 1972–81, 1257 ($\bar{x}$ = 140/year, range 74–180) wolf complaints were reported to Fish and Wildlife District offices. Complaints were investigated, verified or rejected as predation and the offending predator species noted. Complaints included missing animals, discovered carcasses where the cause of death was unconfirmed, harassment or sightings, and confirmed wolf attacks. Bjorge (unpubl.) reviewed 496 such complaints in the Peace River region; 177 (36%) were rated as confirmed wolf attacks. Harassment and missing animal complaints were often precipitated by past losses to wolves.

Analysis of 379 approved claims during 1974–80 [Alberta Predator Indemnity Program (PIP)] indicated that 92% of the claims involved cattle, 5% sheep, 2% swine, 1% goats, and <1% poultry (dogs and horses are not covered by PIP). In the Peace River region Bjorge (unpubl.) reviewed District complaint records and found 80% involved cattle, 6% sheep, 5% dogs, 5% swine, 2% poultry, 1% goats, and 1% horses.

Of 213 confirmed PIP claims, 68% occurred on private lands and 32% on leased public lands. Of 363 approved claims, including confirmed, probable, and "missing only" claims, 152 (42%) occurred on grazing leases on public lands (88% of "missing only" claims were on grazing leases). In northwestern Alberta, where leases are more common, Bjorge (unpubl.) noted 74% of 129 confirmed wolf attacks on cattle occurred on grazing leases.

In BC, production of livestock occurs along narrow cultivated river bottoms surrounded by forests with populations of wild ungulates and wolves, on large semi-forested grasslands of the interior, and around isolated settlements. Occurrences of livestock depredations increased in BC during the 1970s, partly related to recent increases in numbers of wolves following cessation of concentrated wolf control during the 1950s (1979, Min. Environ., BC, unpubl. rep.; Tompa 1980).

Four hundred and thirty-one confirmed wolf–livestock complaints were received by the Fish and Wildlife Branch during 1978–80 ($\bar{x}$ = 144, range 113–174 — Tompa, this publication). Other wolf depredations are known to occur, especially on remote, forested pastures; most are reported as missing animals (Tompa, this publication).

Of 427 confirmed complaints 136 (32%) occurred on public lands ("native ranges" or "forests") and 68% on private lands, including 237 (56%) on "cultivated pastures", 20 (5%) on "intensive crop", 28 (7%) on "rural settlement" and about 1% on other land categories. Of 402 animals killed, 64% were cattle, 17% sheep, 7% horses, 5% dogs, 3% poultry, 2% goats, and 2% swine, rabbits, and others.

4. Seasonal occurrence

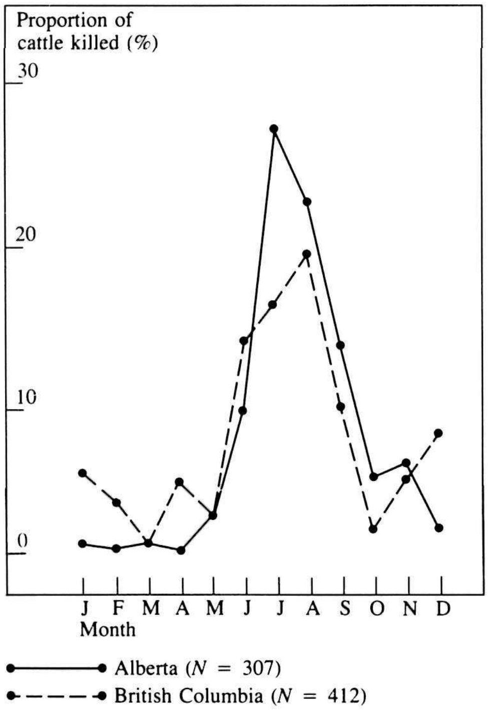
Data from Alberta and BC (Fig. 2) indicated greatest occurrences of wolf–cattle kills during July–August. In Alberta (PIP, 1974–80) seasonal losses of calves compared to older cattle were similar; whereas in BC (Tompa, this publication) most (71%) calf losses to wolves (kills and maulings) occurred during summer months and seasonal variation of losses of older cattle was not pronounced. Dorrance (in prep.) examined PIP data in Alberta during 1974–78 and reported greatest losses of cattle during August and September.

Winter losses to wolves of more cattle in BC than in Alberta are probably related to the proximity of wolves to winter pastures in that Province (Tompa, this publication). Winter losses in BC may also be higher because the Alberta data include proportionately more losses from remote grazing leases, utilized only during summer; most cattle are placed on remote pas-

Figure 2
Seasonal occurrence of confirmed wolf predation on cattle in Alberta and British Columbia

Figure 3
Age- and sex-specific stocking rates and wolf-killed cattle in Alberta

Figure 2



tures during May and removed during October. Despite expected vulnerability of young calves during May and June, reported wolf kills are not as frequent as later in the summer. Denning of wolves during May and June restricts wolf movements, probably resulting in less association with cattle than later in summer. In addition, young cervids may be easier to kill than cattle calves.

In Alberta, 96% of 110 sheep killed by wolves, of which 38 (35%) were lambs, occurred on 18 claims during July–October with no significant monthly variation during the pasture season. Seventy-two additional sheep (46% lambs) were reported missing on these 18 claims. Losses of sheep in BC were also most common during the grazing season (Tompa, this publication).

Thirty-one swine were killed and eight injured on eight confirmed claims in Alberta. Six claims occurred during July–September and two in December. Seasonal variation is not obvious in kills of horses in Alberta and BC, but is with dogs, most of which are killed during winter months (PIP; Bjorge, unpubl.; Tompa, this publication).

5. Prey selection

Of 377 confirmed wolf-kills of cattle in Alberta during 1974–80, 62% were calves, 15% yearlings, 23% cows, and 0.2% bulls (Fig. 3). Bjorge (unpubl.) recorded age- and sex-specific stocking ratios in northwestern Alberta: calves 40.5%, yearlings 12.3%, cows 45.7%, and bulls 1.5% (N = 21 243). Using these figures as representative of stocking ratios in all fringe areas of the province, both calves and yearlings were killed by wolves at greater rates ($P < 0.001$) than cows (Fig. 3). In BC, 66% of 260 wolf-killed cattle were calves, 31% yearlings and cows, and 3% bulls (Tompa, unpubl.).

Wolves apparently do not select lambs over ewes in Alberta; 42% of 79 sheep killed during May–September were lambs (availability is about 96 lambs/100 ewes; M. Dorrance, pers. comm.). Rams are occasionally killed by wolves, including a case where a lone wolf entered a pen with five rams, killed four and severely injured the fifth (C. Cross, pers. comm.).

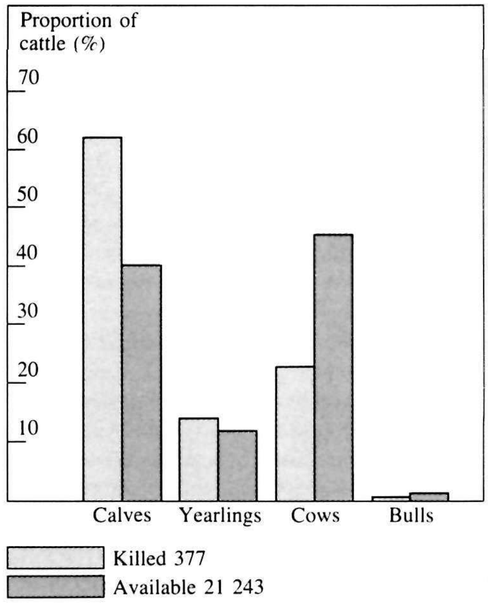
Excessive killing of livestock by wolves occasionally occurs. In 1981 a pack of seven wolves killed or severely mauled numerous sheep in central Alberta; 20 were killed or had to be destroyed. Investigators reasoned this was an instance of pups being taught to kill (R. Hanson, pers. comm.).

6. Management of wolf–livestock conflicts

6.1. Predator indemnity program

Of the four western provinces, only Alberta compensates agriculturists for losses of livestock to predators; livestock losses to wolves are indemnified elsewhere, such as in Italy (Zimen and Boitani 1979), Minnesota (Fritts, unpubl.) and Ontario (Kolenosky, this publication). Initiated in 1974 but retroactive to 1972, the Alberta program covers only food-producing animals. Standard livestock values, based on

Figure 3



current markets, are established annually (e.g. "cow" 1974 — $300, 1977 — $500, 1979 — $700). Market value of the loss must exceed $100. Claims are reviewed by one of two regional committees composed of private producers and governmental representatives from animal health, production, and wildlife management. Losses are judged as "probable" or "confirmed" with corresponding levels of compensation, 50 or 80% respectively. "Loss" includes fatality, injury from which recovery is deemed improbable and disappearance of animals in conjunction with confirmed kills or injuries. Payments for missing animals are not approved unless wolf predation has been confirmed in the area. Complaints are investigated on site by problem-wildlife personnel; predator involvement is noted and recommendations for compensation are recorded on claim forms. Although claim rejection data were not summarized on a case-specific basis (i.e. identification of the predator), the rejection rate of 2776 predator claims during 1976–80 was 22%.

During 1974–80, 384 wolf–livestock claims were approved for payment [19 are excluded from the following analyses because they were special "missing only" claims from the Simonette wolf–livestock project (Bjorge and Gunson, this publication)]. Of the 365 remaining claims, 244 (67%) included confirmed kills, 67 (18%) were judged as probable, and 54 (15%) were "missing only" animals. Claims with confirmed and probable losses also contained missing animals; of payments approved in respect of 2347 animals, 1636 (70%) were missing. Inclusion of that many missing animals in approved claims may be justified as most livestock killed by wolves, at least on remote pastures, are probably never discovered (Bjorge and Gunson, this publication). A mean of 6.4 animals/claim were reported lost on the 365 claims.

A mean of $956 (range $648–$1520) was paid on 319 claims during 1975–80. Yearly fluctuations of money paid (range $29 828 in 1976 to $85 122 in 1979) relate to number of claims, a gradual increase in market values between 1975 and 1980, and yearly differences in proportions of confirmed, probable, and missing claims.

The program provides data on livestock predation and opens up channels of communication with agriculturists. To some extent the program may also produce a greater appreciation of wildlife and wildlife management by farmers and ranchers.

6.2. Other management programs

Wolf control has been the major governmental program to reduce wolf predation on livestock in western Canada. Historically, much of this control has been preventive, i.e. wolves removed in general areas to reduce subsequent losses, rather than reactive. Although all western provinces profess to practise site-specific reactive control, preventive control has been utilized in recent years in Manitoba (Stardom, this publication), BC (Tompa, this publication), and Alberta. Most wolves taken in wolf control in Alberta during the 1970s were removed during winter, several months following depredations. Such control is partly reactive and partly preventive. In some regions in BC wolves are trapped and snared around attractor baits during winter to reduce numbers in problem areas (A. Lay, pers. comm.).

In all four provinces, control has employed trapping or snaring, shooting, and the use of poisons. Cyanide (in guns or otherwise) and strychnine have been used in all provinces. Since 1979 the only chemical predacide allowed for use in BC by provincial regulation is sodium monofluoroacetate (Compound 1080 — see Tompa, this publication), primarily because of its apparent greater selectivity for canids.

Trapping has much potential in both reactive (S. Fritts 1981, US Fish and Wildl. Serv., unpubl. rep.; Kolenosky, this publication) and preventive wolf management. To encourage intensive fur harvests of wolves in fringe areas, wildlife agencies in western Canada need to emphasize wolf-trapping extension programs similar to that recently initiated in Saskatchewan (W. Runge, pers. comm.). Techniques of leg-holding trapping of wolves during winter were developed and demonstrated to trappers. Recreational hunting and commercial trapping have been largely ineffective in preventing wolf depredations despite liberal hunting and trapping regulations. I estimate less than 100 wolves are taken annually by recreational hunters in Alberta.

Alberta and BC appear to have more diverse management programs and more specialized problem-wildlife personnel to investigate and manage depredations by wildlife (Roy and Dorrance 1976; J. Gurba and D. Neave 1979, Alta. Agric. & Fish and Wildl. Div., unpubl. rep.; Tompa, this publication). In Alberta a Problem Wildlife Committee with provincial wildlife and agricultural representatives has planned policies and programs since 1973. In BC a provincial and several regional predator management advisory committees were established in 1974 (Tompa 1980). Management of wolf depredations remains difficult, partly because of the continued grazing of cattle on remote forested public lands where supervision and access are limited.

In western Canada, where large areas of public lands are suitable for grazing, wolf–livestock predation will continue for a long time. Wildlife managers must work closely with ranchers and agricultural organizations to encourage predation-preventive animal husbandry and promote values of all wildlife species including predators.

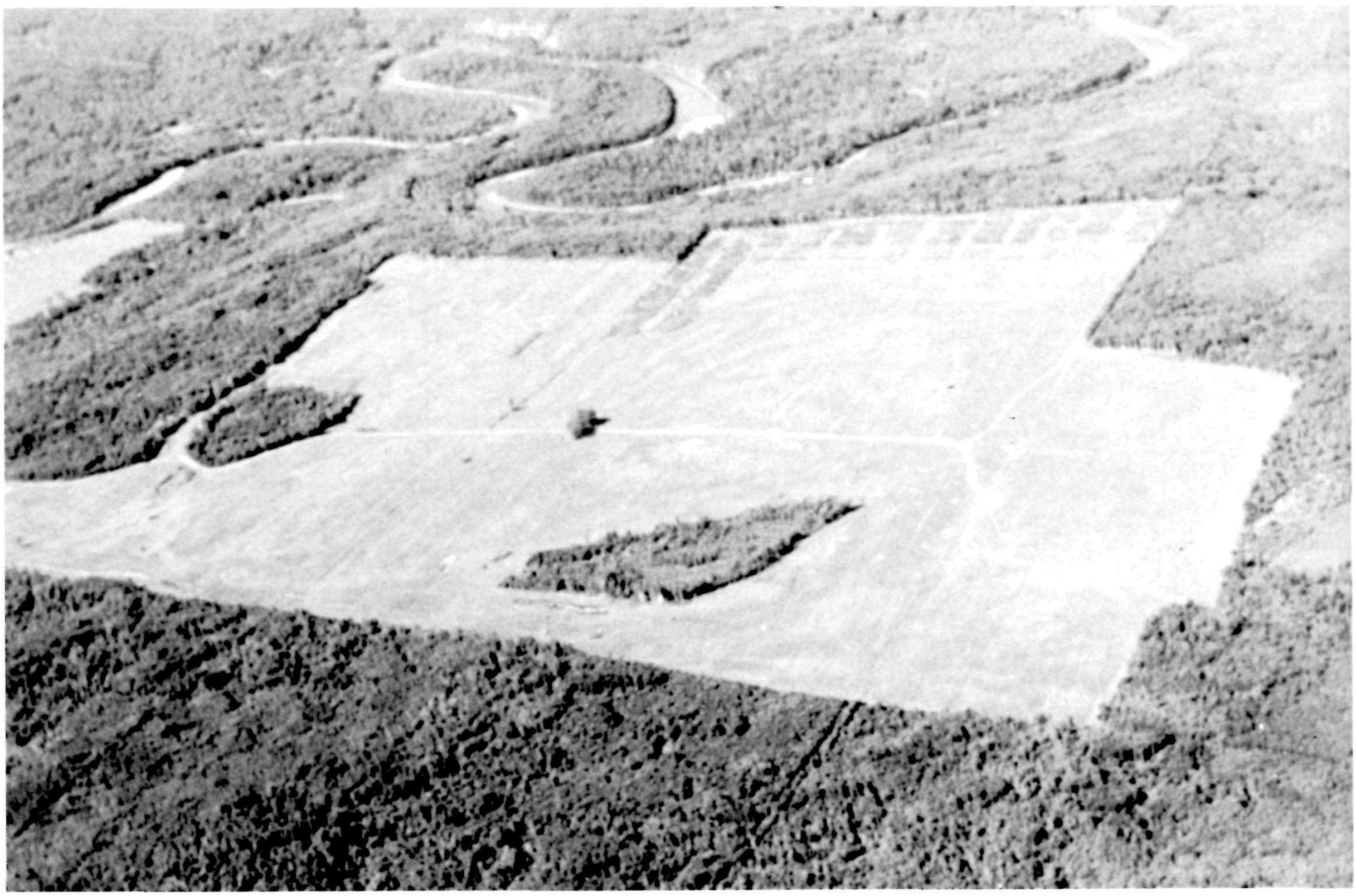
7. Acknowledgements

I am most grateful to Frank Tompa who kindly provided data concerning wolf–livestock predation in BC. Sincere thanks are expressed to A. Lay, D. Pastuk, W. Runge, and H. Strom for providing information from their provinces. I thank R.R. Bjorge, L.N Carbyn, R. Hanson, and R.O. Peterson for helpful reviews of this paper.

Wolf predation of cattle on the Simonette River pastures in northwestern Alberta

The greatest wolf–livestock depredation problems occur along forest–agricultural transition zones. Proper land-use planning can reduce such problems (photo: J.R. Gunson)

R.R. Bjorge
J.R. Gunson



1. Abstract

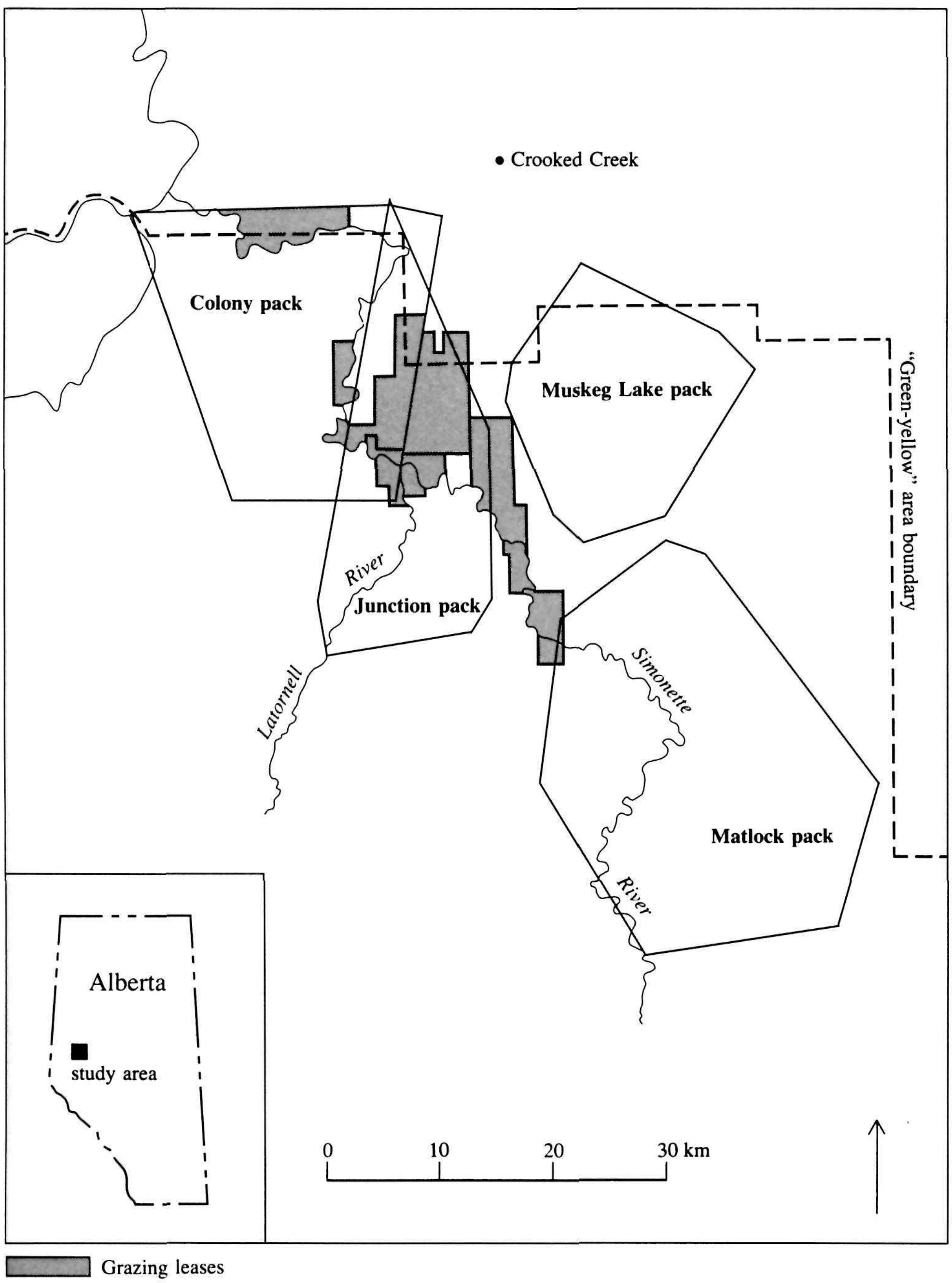
Wolf predation of cattle on 152 km^2 of remote forested grazing leases along the Simonette River (54°55′N, 177°50′W) in northwestern Alberta was studied during 1975/81. Wolves, in a period without controls, increased from approximately 15 in 1975/76 to about 40 in 1979/80. Lone wolves and a pair were located significantly more often on or near (<1.6 km) grazing leases during summer than were packs. Territories of packs were greater during winter (503 km^2, N = 6) than summer (263 km^2, N = 6). Wolves killed 16 of 38 cattle where the cause of death was known and mauled another 51. The summer diet of wolves consisted of cervids in preference to cattle; during the winter cervids constituted 93% of prey occurrences. Wolf control by strychnine poison during winter 1979/80 reduced the number of wolves to about 13. Known numbers of cattle mauled (8) and killed (3) in 1980 following wolf control were reduced from previous years. Mortality of cattle varied from 2.9% (of 2288) in 1976 to 3.7% (of 1558) in 1979, then decreased to 2.5% (of 1772) following wolf control. Winter wolf control may not remove offending lone wolves because they range more widely than packs and often vacate grazing leases during winter.

2. Introduction

In North America it has long been recognized that wolves kill domestic livestock (Young and Goldman 1944, Pimlott 1961). Wolf predation on livestock has been reported in Eurasia as well, including Fennoscandia (Haglund 1975), Italy (Boitani and Zimen 1975), the Soviet Union (Bibikov 1975) and Yugoslavia (Bojovic and Colic 1975). Ensuing conflicts between agriculturists and wolves have been partially responsible for wolf control programs (Young and Goldman 1944). In Alberta, wolves occupy about 404 000 km^2 or 61% of the Province's area (Gunson, this publication). Although most occupied range is unsettled for-

Figure 1
Territories of four wolf packs on or near grazing leases, Simonette River area, northwestern Alberta, 1979–80

Figure 1



est, predation of livestock occurs along the extensive forest–agriculture fringe (Bjorge 1980; Gunson, this publication) and within forested areas under lease to cattle ranchers. Knowledge of wolf–livestock predation is limited as the subject has not been studied extensively. This paper summarizes field research of wolf–cattle predation on remote grazing leases in the Simonette River area of northwestern Alberta.

3. Study area

The study area included seven grazing leases ranging in size from 5 to 59 km^2 (Fig. 1). All leases were located on crown lands in the vicinity of the forest–agricultural fringe along the Simonette River in the southern portion of the Peace River area of Alberta. Two leases bordered directly on deeded agricultural land and forested crown land while five leases were 4–20 km into forested Crown lands. Numbers of cattle pastured on leases during the May–October grazing season varied from 1558 in 1979 to 2288 in 1976. Mean annual density was 12–15 cattle/km^2. Cattle were not present during winter months.

The area is within the boreal forest (Rowe 1972); trembling aspen (*Populus tremuloides*) is the dominant tree species, balsam poplar (*Populus balsamifera*), willow (*Salix* spp.) and alder (*Alnus* spp.) being common. The topography of most of the area is generally flat, but is interrupted by the banks (up to 120 m in depth) of numerous creeks and the Simonette and Latornell rivers.

Wild ungulates were common, especially moose (*Alces alces*)(1.3/km^2 — Bjorge, unpubl. data); elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*), and mule deer (*Odocoileus hemionus*) were locally abundant. Beaver (*Castor canadensis*) and black bear (*Ursus americanus*) were common.

4. Materials and methods

We trapped wolves with 48 and 114 Newhouse traps or neck snares similar to those used by Nellis (1968) for coyotes (*Canis latrans*). Captured wolves were restrained with a modified hay fork or forked stick; we then measured, examined, radio-collared (AVM Instrument Company, Champaign, Illinois), and released them at the capture site. Wolves were relocated from fixed-wing aircraft, usually twice a week during May–October and weekly during other months. Locations were plotted on forest cover maps and maximum ranges for any specified period were determined by the minimum area method.

We recorded wolf tracks observed during winter to help determine approximate numbers and locations of wolves. We recorded all reports of wolf mortality. We determined food habits by collecting and analysing scats and observing kills. Wolf scats were distinguished from those of coyotes by size (Weaver and Fritts 1979) or presence of wolf sign. We counted cattle entering and leaving leases, examined them for signs of attacks by wolves or bears and occasionally observed cattle on the leases. Dead cattle were observed by study personnel or reported by cattlemen. Only cattle with obvious signs of attack, e.g. teeth or claw marks or blood trails, were classified as predator kills. Bite marks were evident on cattle killed by wolves; wounds from claws were evident on cattle killed by bears. Two cattle, which had been severely mauled by wolves, were subsequently killed by cattlemen and were classified as wolf kills.

During 1976/80, in lieu of governmental wolf control, cattlemen were compensated for losses through a special program of the Alberta Predator Indemnity Program (PIP) at 100% of annually established standard livestock values for confirmed predator kills, and at 80% for all other cattle missing in fall. Standard PIP compensation is based on 80% for confirmed kills and 50% for probable kills (Gunson, this publication). Governmental wolf control was then resumed on the study area in 1979/80. Wolf control and standard PIP were available prior to onset of this research in 1976.

Chi squared tests were used to determine differences in the frequency of relocation of lone and pack wolves on cattle leases and to establish age-specific mortality of cattle.

5. Results and discussion

5.1. Wolf numbers and territories

Numbers of wolves on the study area increased from an estimated 14–15 during midwinter 1975/76 to 39–40 during midwinter 1979/80 (Table 1). This increase was probably a recovery following governmental wolf control, which removed at least 11 wolves during 1973/74. Mean pack size during early winter for 5 radio-tracked packs, over a total of 10 pack winters, was 6.9 (range 3–12).

Lone wolves were present each year. Based on observations of tracks during winters 1975/79, 6–20% of the population was comprised of lone wolves. Of 21 wolves killed during the 1979/80 control program, 3 (14%) were classed as lone wolves. These figures are comparable with those for central Alberta given by Fuller and Keith (1980), who calculated occurrences of lone wolves at 17%.

Table 1
Trends in numbers of wolves in mid winter on the Simonette River area of northwestern Alberta during 1975–81*

Winter	Estimated no. of wolves	No. of packs†	Lone wolves
1975–76	14–15	3	2–3
1976–77	23–25	3	2–3
1977–78	29–33	5	2–3
1978–79	28–31‡	5	2–3
1979–80	39–40 (12–13)§	7	3–4
1980–81	15–16	2	3–4

*From radiotelemetry and snow tracking.
†Including pairs.
‡Six wolves were illegally removed during 1978.
§Following wolf control.

Territories of all packs were smaller in summer (May–Oct.) than in winter (Nov.–Apr.)(Table 2). This is in contrast to findings by Cowan (1947), who reported that summer wolf range in Jasper National Park, Alberta, was larger than winter range. However, Carbyn (1975*a*) concluded that winter range of wolves in the same area was larger. Three radio-tracked packs ranged in territories averaging 263 km^2 over six summers and 503 km^2 over the following winters. Ranges of lone wolves were generally greater than those of packs. The mean range of four lone wolves monitored during summer and winter (mean of 261 days) was 2322 km^2. Jordan *et al.* (1967) and Van Ballenberghe *et al.* (1975) reported that lone wolves travelled within the territories of several packs, as was the case here.

Density of wolves in two packs during winter 1978/79 was 1 wolf/71 km^2; density of four packs during winter 1979/80 was 1 wolf/47 km^2. These estimates, which do not include any lone wolves within winter pack territories, are

Table 2
Summer and winter ranges of wolves on the Simonette River area of northwestern Alberta

Wolf/pack identity	Period	Territory size (km^2) Summer			Winter		
Matlock	1976–77	232	(Jun 19–Oct 26)	22*	735	(Nov 2–Apr 20)	25*
	1978–79	476	(July 18–Oct 31)	64	878	(Nov 2–Apr 20)	54
Colony	1978–79	265	(May 3–Oct 31)	46	334	(Nov 3–Apr 26)	34
	1979–80	317	(May 2–Oct 31)	59	386	(Nov 2–Apr 29)	91
	1980–81	183	(May 5–Oct 31)	80	403	(Nov 3–Jan 30)	31
Junction	1979–80	104	(Aug 20–Oct 31)	60	297	(Nov 3–Feb 21)	109
	1976–81	263		56	503		58
Lone 2	1976–77	1639	(Aug 9–Oct 26)	18	2404	(Nov 2–Apr 26)	21
Lone 8	1978–79	1151	(May 9–Oct 31)	38	689	(Nov 2–Feb 28)	14
Lone 21	1980–81	535	(July 22–Oct 1)	11	79	(Nov 12–Apr 30)	19
Lone 22	1980–81	318	(July 24–Oct 31)	11	1348	(Nov 2–Apr 30)	23
	1976–81	911		20	1130		19

*Number of radio locations (fixes).

greater than other reports from Alberta. Fuller and Keith (1980) estimated densities of packs near Fort McMurray, Alberta, at 1 wolf/158 km^2 and near Swan Hills, Alberta, at 1 wolf/90 km^2.

5.2. Occurrence of wolves on grazing leases

Four lone wolves, one pair and one wolf trailing from its pack were radio-located on or near (<1.6 km) grazing leases during 46% of 124 fixes when cattle were present and during 5% of 121 fixes when cattle were absent (Table 3). By contrast, wolves belonging to packs were located on leases during 31% of 338 fixes when cattle were present and during 22% of 374 fixes when cattle were absent. The differences in summer locations between lone and pack wolves were significant ($P < 0.01$), suggesting a greater tendency for lone wolves to associate with cattle.

The behaviour of wolf 2, an adult female, was somewhat typical of other lone wolves. During summer of 1976, wolf 2 was located on grazing leases 7 of 16 fixes although <10% of her 1639 km^2 range was within grazing leases. After the removal of cattle during late October, she left the study area in early November, crossed a major highway, and occupied an area about 50 km to the north of her previous range. During winter she was radio-located within 1.6 km of farmyards with cattle 5 of 16 times.

Of three packs monitored over a total of 7 years, only the Junction pack regularly associated with cattle during one summer (77% of 60 fixes when cattle were present and 24% of 109 fixes when cattle were absent). This pack left the grazing lease within 3 days of the removal of cattle in fall 1979 and moved to an adjacent lease with cattle.

Thirty one (79%) of 39 scats collected during summer 1979 from one rendezvous site within the territory of the Junction pack contained remains of cattle. In contrast, during summer of 1979, cattle remains occurred in only 9 (17%) of 52 scats from two rendezvous sites of the Colony pack and 0 of 21 scats from one rendezvous site of the Muskeg Lake pack. The apparent predation of the Junction pack on cattle was related to its summer range being almost entirely (86%) within grazing leases. By contrast, only 15% of the summer ranges of two other packs (Matlock and Colony), during a total of six summers, included grazing leases.

Six or fewer cattle were missing at round-up (end of summer period) from grazing leases within the territories of radio-collared packs during five of seven summers, suggesting that packs usually do not prey heavily on cattle. These included the Matlock pack during 1976, 1978, 1979, and the Colony pack during 1978 and 1979. Although four of seven packs killed at least one head of cattle each, they were primarily dependent on wild prey.

Following removal of primarily pack wolves (only 3 of 21 wolves were lone animals) during the 1979/80 control program, cattle mortality decreased in 1980 (Table 4). During summer 1980, lone wolves were more common on the study area than during previous summers; 3 of 5 wolves captured during 1980 were lone compared to 0 of 10 in 1979 and 1 of 6 in 1978. Although lone wolves were more dependent on cattle than packs, total predation by wolves in packs may have been greater than that of lone wolves. Also, perhaps some of the lone wolves present in 1980 had not yet learned to kill cattle.

Table 3
Occurrences of radio-located lone, paired and pack wolves on or near (<1.6 km) grazing leases in the Simonette River area, northwestern Alberta

Status	Wolf/pack identity	Occurrence on or near grazing lease: Grazing period	Non-grazing period
Lone	2	7/18*	1/21
	8	15/38	0/14
	21	6/11	0/19
	22	6/11	0/23
	25	–	0/19
	13	13/31	5/25
Pair	1	10/15	–
Total		57/124 (46.0%)	6/121 (5.0%)
Pack	Matlock	10/93	8/109
	Colony	50/185	47/156
	Junction	46/60	26/109
Total		106/338 (31.4%)	81/374 (21.7%)

*Seven of 18 radio-locations were on or near grazing leases during the grazing period.

6. Food habits

Cattle remains occurred in wolf scats only during the grazing period (Table 5). Cervid remains occurred in scats during both the grazing and non-grazing seasons, but most frequently during winter. There were cattle remains in 50 (20%) of 245 wolf scats collected during 1976/80. Wolves scavenged from at least 15 of 34 cattle carcasses resulting from bloat, poisonweed, bear kills, and unknown causes. Carcasses of cattle killed by wolves were completely consumed, primarily by wolves.

7. Cattle mortality

Total mortality of cattle while on grazing leases increased from 2.9% in 1976 to 3.7% in 1979 (Table 4). During the period of no wolf control, the general mortality was significantly greater ($P < 0.001$ in both cases) for 0–12 month calves (5.8%) and yearlings (3.3%) than for adults[1] (1.3%).

[1]More than 2 years old.

During the study period an analysis of cattle mortality shows that in 38 cases where the cause of death was known, 16 (42%) of the cattle died from wolf predation, 4 (11%) from black bear predation and 18 (47%) from other causes such as poisonweed, bloat, and pneumonia. Most of the dead cattle were not found because of the remoteness and large size of the leases and the heavy tree cover. We suspect that cattle killed by predators were more difficult to discover than cattle dying from other causes because they were more completely consumed. Carcasses of adult cattle were more likely to be found than those of younger cattle. For example 36% of all adult cattle missing were found dead, compared to only 7% of all missing calves. Results from this study (Table 6) and throughout northwestern Alberta (Bjorge, in prep.) indicated that calves and yearlings were killed at greater rates than adults (see Gunson, this publication). Thus, the cattle most often killed were less likely to be discovered. Our estimate of cattle dying from wolf and bear predation may therefore be low.

Following wolf control during winter 1979/80, which reduced the number of wolves by approximately 70%, the rate of cattle mortality decreased from 3.7% in 1979 to 2.5% in 1980 (Table 4). Assuming other mortality factors were approximately equal in 1979 and 1980, the reduced wolf predation would seemingly account for the lower mortality rate. Bjorge (in prep.) compared cattle mortality on intensively managed, largely predator-free Provincial Grazing Reserves (PGR) in northwestern Alberta with that on the Simonette pastures. Total losses on the PGR during 1976–79 averaged 1.2% mortality compared to 3.3% on the Simonette study area during the same period. If mortality from other causes was equal on the two areas, then maximum mortality from predators (wolves and bears) would be approximately 2.1% on the Simonette pastures (Table 7).

Table 4
Yearly loss and mauling rates of cattle to wolves on grazing leases in the Simonette River area, northwestern Alberta

Year	Cattle on study area	Total loss (%)	Cattle mauled by wolves	Cattle killed by wolves*	Wolves present
1976	2288	2.85	6	1	23–25
1977	2023	3.46	5	1	29–33
1978	1784	3.58	13	3	28–31
1979	1558	3.65	19	8	39–40
1980	1772	2.48	8	3	16–17†

*These include known wolf kills only; other kills by wolves occurred but were not recorded.
†Wolf control removed 21 wolves and 6 others were shot, trapped, or found dead during 1979–80.

8. Age and sex of cattle attacked

Wolves often kill young, old, or disabled prey (Fuller 1962, Pimlott *et al.* 1969, Mech 1970). In our study significantly greater ($P < 0.001$) proportions of calves and yearlings were attacked (killed or mauled) than adults (Table 6). No disabilities were obvious among the calves or yearlings killed. However, two of five cows killed were in poor health prior to attack; one was weak and lame and the other was sick and had been separated from the herd. These data suggest that wolves do not kill cattle at random, but select young, inexperienced, or disabled cattle, leaving healthy adults relatively immune to predation.

The main point of attack on cattle was the hindquarters including the tail, vulva, and lower thigh. Occasionally cattle were attacked on the face, including the nose and ears, behind the front legs, in front of the rear legs, and on the belly.

9. Concluding discussion and management recommendations

Cattle pastured during summer represent a concentration of potential prey for wolves. Although lone wolves and one pack appeared to rely substantially on the Simonette cattle, wolves in other packs did not. The limited dependence on cattle by packs was probably re-

Table 5
Dietary items in wolf scats from trails in the Simonette River area, northwestern Alberta

	Scats (%)											
	Grazing period (May–Oct)						Non-grazing period (Nov–Apr)					
Dietary item	1976 (*N* = 37)	1977 (*N* = 45)	1978 (*N* = 73)	1979 (*N* = 60)	1980 (*N* = 30)	1976–80 (*N* = 245)	1975–76 (*N* = 18)	1976–77 (*N* = 70)	1977–78 (*N* = 80)	1978–79 (*N* = 41)	1979–80 (*N* = 70)	1975–80 (*N* = 279)
Cattle	32.4	11.1	15.1	21.5	30.0	20.4	0.0	0.0	0.0	0.0	0.0	0.0
Cervid	54.0	66.6	56.2	40.0	30.0	50.6	100.0	98.6	83.8	92.7	96.0	92.8
Beaver	21.6	24.4	28.8	20.0	6.7	22.0	5.6	0.0	7.5	4.9	5.7	4.7
Hare	5.4	17.5	28.7	36.7	57.0	28.6	0.0	2.9	15.3	12.2	31.4	14.6
Bird	13.5	15.5	4.1	8.3	3.0	8.6	0.0	2.9	8.7	2.4	1.4	3.9

Table 6
Cattle killed and mauled by wolves on grazing leases in the Simonette River area, northwestern Alberta, 1976–80

	No. of cattle (%)			
Cohort	On study area	Mauled	Killed	Total
Calf	3448	28 (0.81)	8 (0.23)	36 (1.04)
Yearling	1925	15 (0.78)	3 (0.16)	18 (0.94)
Cow	3913	8 (0.20)	5 (0.13)	13 (0.33)
Bull	140	0 (0.00)	(0.00)	0 (0.00)

Table 7
Cattle mortality from predators and other causes in the Simonette River area, northwestern Alberta

	Cause of death		
Cohort	Wolves	Bears	Others*
Cow	5	0	9
Calf	8	1	6
Yearling	3	3	3
Bull	0	0	0
Total	16	4	18

*Includes bloat, poisonweed, and pneumonia.

lated to an abundance of wild prey, and to the limited overlap between summer territories of packs and grazing leases.

The suggestion that lone and paired wolves are more dependent on cattle than packs is noteworthy and has important implications for wolf control. The main technique used in Alberta to remove wolves that kill cattle during summer is the use of strychnine poisoning during winter. Control during winter does not always remove problem lone wolves. This is because lone wolves travel widely and appear to avoid the grazing leases when cattle are absent. In contrast, packs tend to occupy the same general area during both winter and summer, although winter territories are considerably larger. Packs on expanded winter ranges are relatively vulnerable to strychnine baits, whereas highly dispersed lone wolves are not. Investigators of livestock killed by wolves should attempt to establish whether a lone wolf or a pack was the cause.

Greater emphasis should be given to site-specific wolf control in summer instead of the current control in general areas of grazing leases during winter, particularly where lone wolves are involved. Grazing leases should not be located beyond a few kilometres of the forest–agricultural fringe. Lessees should be notified before being given a lease or a lease renewal that losses to wild predators can be expected. Only healthy animals should be pastured on grazing leases; sick animals should be treated or removed.

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Problem wolf management in British Columbia: conflict and program evaluation

Frank S. Tompa

1. Abstract

During 1978–80, 420 livestock, 13 domestic dog, and 19 instances of human safety related wolf complaints were reported in BC. Wolves do not threaten the livestock industry, but have a serious impact on individual producers. Beef calves are the most important domestic prey of wolves and most livestock losses occur in the summer/fall season. Many harassment complaints are received in the winter, when wolves are visible close to rural settlements. Husbandry practices may influence wolf–livestock interaction. Problem wolves, which represent 5% of the provincial wolf population, do not seem to depend on domestic prey for their survival. Control is most effective when it is directed at wolves involved in attacks on livestock, and least effective when action is taken in response to harassment reports. The present site-specific, reactive control program does not threaten the provincial wolf population. Management flexibility through a variety of actions is essential to reduce wolf–human conflicts to acceptable levels and to prevent the uncontrolled taking of wolves by illegal means.

2. Introduction

The wolf (*Canis lupus*), considered vermin in BC until 1955, is now officially recognized as a valuable component of provincial wildlife and is protected by restrictive hunting and trapping regulations (Preliminary Wolf Management Plan[1], Min. of Environ., BC, 1979). Wolves are abundant in most areas of the Province and locally cause concern for human safety as well as to livestock owners. Such conflict areas are sporadic, often isolated, and usually restricted to valley bottoms, interior grasslands, and other situations where marginal agricultural potential often exists within an immense area of wilderness and mountain ranges.

Ministry policy on management of problem predators, introduced in 1979, establishes that wolves can only be controlled on a site-specific basis where there are verified attacks on, or harassment of, domestic animals and threats to human safety (Tompa, this publication). The policy requires that, wherever possible, conflict with livestock be resolved through improved husbandry practices and that control be directed at individual wolves and packs causing a local problem. Management must be flexible in response to a variety of local circumstances. The policy was designed to fulfil Ministry management objectives rather than to provide experimental research information on the subject.

The purpose of this paper is to examine the applicability and effectiveness of various wolf management methods within the limits of existing policy.

3. Methods

Data were largely obtained from problem-wildlife complaint forms. These forms were introduced on 1 January 1978 to facilitate computer processing of data. They are completed by trained Ministry personnel who investigate complaints, implement management programs and make recommendations.

A distinction is made between wolf attacks and wolf harassments. The former result in death or injury; the latter represent instances where although no actual damage has occurred, the presence of wolves could be perceived as either an actual or a potential threat to humans and domestic animals. Complaints were rejected where wolf presence could not be confirmed.

Financial loss to livestock producers is calculated on the basis of annual average losses in various livestock classes and the livestock market prices in January of each year. Injuries from maulings depreciate market values and may necessitate premature slaughter of stock. Veterinary and added investments costs can be substantial; therefore maulings are grouped with kills as a financial loss.

Data from 1978, 1979, and 1980 only were used for annual comparisons and to indicate seasonal trends. Data from 1 Jan. – 31 Mar. 1981 were included only where the pooling of information did not introduce a bias. Data from all parts of the Province were pooled to assess and describe various aspects of wolf–human conflicts and to provide a general picture of control methods and management programs. Data were also grouped on the basis of conflict areas, within which local wolf problems, human activities (e.g. care of domestic dogs, animal husbandry), current wolf management programs, and other contributing factors were interrelated during the recording period. In localities where there were constant wolf problems, conflict areas were determined from data on the activities of the same wolf pack, or a succession of packs, affecting the same group of complainants.

The effectiveness of wolf control, following documented livestock loss, is rated as high, moderate, or low when no further loss is recorded for 1 year, 6 months, or 3 months respectively. Where wolf control follows livestock harassment only, effectiveness is similarly measured by the length of time free of further harassment and with no loss.

4. Results

4.1. Survey results

The Fish and Wildlife Branch of the BC Ministry of Environment recorded 19 human safety, 13 dog, and 420 livestock-related wolf complaints during 1978–80. The number of dogs and livestock killed or mauled by wolves is given in Table 1. Although problems were reported throughout the Province, they were generally concentrated in extensive livestock production areas situated within the provincial wolf range (Tompa, this publication).

Verified wolf-related losses in all important stock classes were consistently less than 0.1% of the respective provincial stock populations (Table 2). The Ministry does not have reliable information on unreported stock losses or losses on remote summer cattle ranges where late reportings of losses prevented verification. However, independent statistics collected by the BC Cattlemen's Association (BCCA 1978–80, unpubl. rep.) indicate that the total number of cattle killed in BC, and attributed by the ranchers to wolves, does not exceed the 0.1% of losses within the Province. The highest level of wolf-related cattle losses claimed by Minnesota ranchers between 1977 and 1980 was 0.045% (S.H. Fritts, pers. comm.).

Between 1 January 1978 and 31 March 1981, 243 individual ranching operations reported wolf–livestock problems at least once,

[1]Referred to throughout this paper as PWMP.

Table 1
Numbers of livestock killed (k) and mauled (m) as verified by Fish and Wildlife Branch personnel, 1978–80, translated into annual financial losses

	1978			1979			1980			Annual average			Value/*	Loss/
	k	m	Total	k	m	Total	k	m	Total	k	m	Total	head ($)	Year ($)
Dairy calf	1	0	1	0	0	0	0	1	1	0.3	0.3	0.7	120	84.0
Dairy cow	1	0	1	1	1	2	3	0	3	1.7	0.3	2.0	1200	2 400.0
Beef calf	45	35	80	65	33	98	63	37	100	57.7	35.0	92.7	180	16 686.0
Beef cow	21	11	42	31	18	49	16	11	27	26.0	13.3	39.3	850	34 405.0
Bull	4	0	4	2	0	2	1	1	2	2.3	0.3	2.1	1150	3 105.0
Colt	2	0	2	6	2	8	0	0	0	2.7	0.7	3.3	400	1 320.0
Horse	10	7	17	4	1	5	5	2	7	6.3	3.3	9.7	700	6 790.0
Lamb	6	0	6	2	1	3	15	0	15	7.7	0.3	8.0	85	680.0
Sheep	24	3	27	19	2	21	1	4	5	14.7	3.0	17.7	65	1 150.5
Goat	8	0	8	1	0	1	0	2	2	3.0	0.7	3.7	60	222.0
Swine	0	0	0	0	0	0	1	1	2	0.3	0.3	0.7	88	61.6
Domestic dog	0	0	0	16	7	23	4	2	6	6.7	3.0	9.7	not available	
Rabbit	0	0	0	0	0	0	1	0	1	0.3	0	0.3	4	1.2
Poultry	1	0	1	0	0	0	11	0	11	4.0	0	4.0	2	10.0
Totals	133	56	189	147	65	212	121	61	182	133.7	60.7	194.3		$66 915.3

1981 January marketing value/animal (Min. of Agric., BC, unpubl. rep.).

including 194 producers who lost stock to wolves; 32 producers who suffered financial losses during 2 calendar years; and three producers who had losses in 1 calendar year, but had their stock harassed by wolves in 2 additional calendar years. Producers with chronic wolf problems represent less than 2.5% of the more than 1500 cattle and sheep operations located within the provincial wolf range.

An average of 60 producers annually suffered wolf-related stock losses, averaging $1120 loss per producer. This loss represents 9–22% of the annual net farm income of a typical ranching operation. (Min. of Agric., BC, unpubl. rep.). If reduced production levels caused by stock losses and increased investment costs are taken into account, the real loss to individual producers may be higher than indicated, and inhibitory if it occurs annually.

Furthermore, most stock losses occur at the edges of agricultural areas and apparently affect ranchers with low to moderate farm incomes. Farms with high incomes seem to be not only better situated, but also their operators are able to hire riders and to exercise other preventive measures, e.g. electric fencing, guard dogs, adequate feed supply, thus minimizing losses from all causes, including predation.

4.2. Wolf–livestock interaction

The distribution of the 420 wolf–livestock complaints showed a characteristic seasonal pattern (Fig. 1) during the 3 years: 180 (43%) complaints were received during a 5-month fall/winter period (Nov.–Mar.) and 202 (48%) during a 5-month (May–Sept.) spring/summer period. Seasonal lows occurred in April and October. Interestingly, only 94 (52%) of the fall/winter complaints related to verified attacks by wolves, i.e. livestock killed or mauled, and 86 (48%) to harassment only. By contrast, 163 (81%) of the spring/summer complaints related to attacks and only 39 (19%) to harassment by wolves (Fig. 1). The difference between the two seasons is highly significant ($P < 0.001$).

The seasonal distribution of attack and harassment complaints correlates with the seasonal distribution and activities of livestock and wolves. During the fall/winter period, most livestock are kept near farm buildings on cultivated pastures and winter feedlots. Not surprisingly, 150 (83%) of the 180 fall/winter complaints related to problems on pastures and feedlots close to farm buildings, and only 30 (17%) to problems on native ranges.

During the spring/summer period, native ranges, i.e. remote sections of private and leased land, forest grazing permit areas, and community pastures, are more intensively used, particularly for beef-cattle grazing. Consequently, 107 (53%) of the 202 spring/summer complaints related to problems near rural settlements and 95 (47%) to problems on native ranges. During the April and October low periods, the 24 and 15 complaints received were excluded as most seasonal changes in livestock distribution take place during those 2 months (Fig. 1).

Winter game surveys (Fish and Wildl. Branch, Min. of Environ., BC, unpubl. rep.) show moose (*Alces alces*), deer (*Odocoileus virginianus* and *O. hemionus*), and wolf concentrations, particularly in those parts of northern and central livestock production areas where

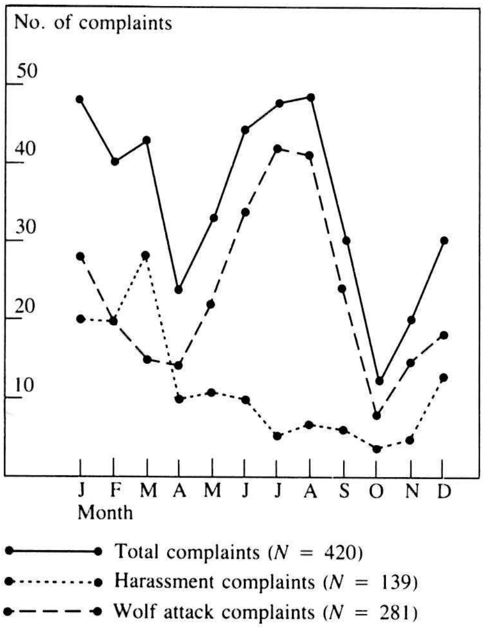
Figure 1
Seasonal distribution of livestock-related wolf complaints, 1978–80

Figure 2
Seasonal distribution of wolf-related livestock losses, 1978–80

at lower elevations cultivated pastures and winter feedlots are interspersed with prime moose and deer winter ranges.

It is suspected that harassment of stock is often reported because wolves or their tracks are seen near farm buildings, not because there is an actual threat to the livestock. This probably accounts for the relatively high number of harassment complaints during the fall/winter period (Fig. 1). It is difficult to determine if

Figure 1



there is a potential threat. During the spring/summer period wolves are not readily observed, particularly on remote native ranges, and most wolf–livestock interaction is detected only after the stock has been killed or mauled.

The above assumption is supported by the fact that the annual harassment/attack report ratio increased from a 1978 low of 0.32 (28:85) to a 1980 high of 0.75 (72:96), while actual livestock losses remained at the same level (Table 1). This increase may reflect in part an increased use of a newly introduced reporting system, and in part a politically motivated response by ranchers to a moratorium on the use of poison baits in wolf control, which lasted from December 1978 until June 1980 (Tompa, this publication), rather than a real increase in wolf-related incidents.

Further support for the assumption is provided by the seasonal distribution of the 541 wolf-related livestock losses (Fig. 2), excluding poultry, domestic rabbits, and dogs; 347 (64%) were killed or mauled during the spring/summer and only 155 (29%) during the fall/winter period. The late winter low of 14 losses coincided with the annual high (Fig. 1) of 28 harassment reports during March. The early fall low of 13 losses conformed with seasonal lows both in harassment and attack reports.

The seasonal distribution of cattle killed or mauled between 1978 and 1980 is shown in Figure 3. Calves were the most important domestic prey of wolves (Table 1). Two hundred (71%) of the 280 calves lost were attacked during the 5-month spring/summer period, in contrast to the 65 (49%) of 132 adult cattle killed or mauled.

The gradual increase in the number of livestock killed or mauled per attack by wolves between March and November (Fig. 4) presumably reflects the proportional increase in the number of young livestock available to wolves as well as the increased food requirements of wolves toward the end of the year, due to the presence of pups in the packs.

4.3. Wolf–dog interaction

The 13 dog-related complaints from 1978–80 refer to 29 dogs killed or mauled by wolves; 9 complaints were of attacks by wolves and 4 were of harassment. During the 3 years, all 29 dogs killed or mauled were attacked by wolves between October and March, presumably because of the closer proximity of wolves to human settlements, as noted earlier[1]. During the first 3 months of 1981, a further 13 dog-related complaints were received, primarily from Vancouver Island, indicating a considerable increase in wolf–dog interaction. It is in-

Figure 2

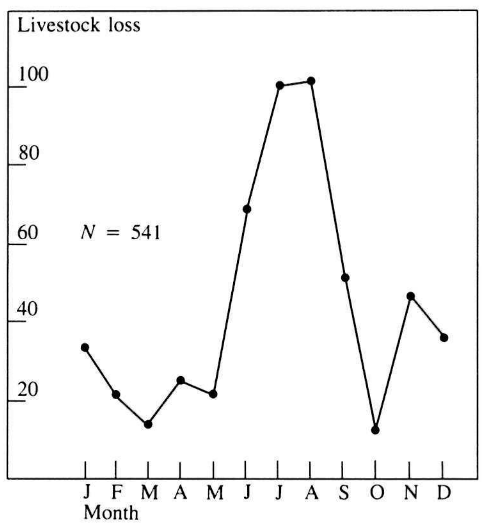


Table 2
Annual wolf-related livestock losses in relation to provincial stock populations (1978–80)

Source	Stock class	$\bar{X}$ loss/year	Stock popn.*	Loss (%)
Fish and Wild. Br. records	Beef calf	92.7	209 500	0.044
	Beef cow	39.3	304 000	0.012
	Horse and colt	13.0	60 000	0.022
	Sheep and lamb	25.0	48 000	0.053
BCCA statistics	Beef calf	158.0	209 500	0.075
	Beef (grown cattle)†	59.0	378 250	0.015

*Min. of Agric., BC, unpubl. rep.; figures represent the mean values between 1980 July and 1981 January stock populations.
†Includes bulls, cows, steers, and heifers.

[1]Wolf attacks on dogs were reported in several isolated areas of Vancouver Island and mainland BC during the 1981 summer.

Figure 3
Seasonal distribution of wolf-related cattle losses, 1978–80

Figure 3

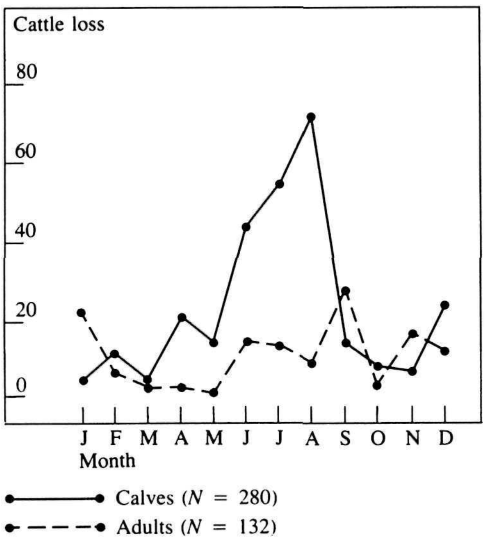
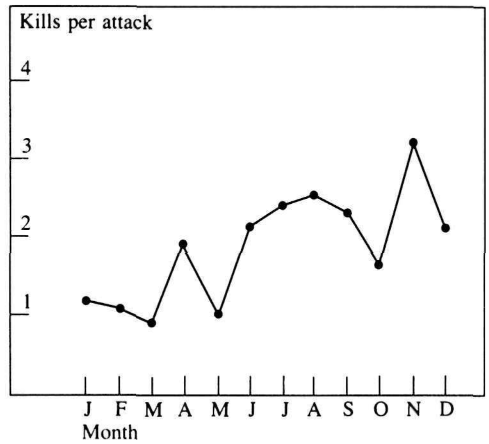


Figure 4
Number of livestock killed by wolves per attack throughout the 1978–80 period

Figure 4



No. kills = 541
No. attacks = 281
Ave. kills/attack = 1.93

teresting to note that 21 (81%) of the 26 wolf–dog complaints were unrelated to other wolf incidents; 5 were associated with other livestock complaints, but only 2 reports referred to dogs attacked by wolves in areas of concurrent livestock losses.

4.4. Wolf–human interaction

With one exception, the 19 wolf complaints concerning human safety were recorded on Vancouver Island, offshore islands, and within adjacent mainland coastal areas. One such encounter reportedly resulted in a light injury to the hand of a woman, who apparently tried to beat off a single wolf approaching her. Another report refers to a forest engineer treed by a pack of wolves for 4 h. The pack left only after one male was shot by a conservation officer. In another incident a pack of wolves ran parallel to two hunters returning to their car. The hunters wounded one wolf, but the pack left only when the car was started.

Information on these and other wolf–human encounters is insufficient to describe them as bona fide attacks or to detect any causal relationship. However, the complaints showed an increasing trend over the 3-year period (1 in 1978, 4 in 1979, and 14 in 1980), which can only be partly explained by an increasing public awareness of wolves. On Vancouver Island and offshore islands the close proximity to human settlements, in areas of high wolf densities, raises the possibility of interbreeding with dogs. Although large-scale genetic contamination of wild wolf populations is unlikely to occur, past records of adverse wolf–human encounters in Europe (Pulliainen 1980, unpubl. rep.) may be explained by the increased aggressiveness of wolf–dog hybrids. Furthermore, in the long-lasting absence of trapping and hunting of wolves on Vancouver Island (Tompa, this publication) the species might have lost some of its characteristic shyness.

The above are only speculative explanations. The risks posed by wolves to human safety within the Province remain extremely low. Common sense dictates that people be careful with any wild animals, particularly as any unusual behaviour may be related to rabies; although wolves in the Province are not infected, bats are known to be an important reservoir of the disease.

4.5. Special distribution of conflicts and pack status

On the basis of information on the complaint forms, including complaints during the first 3 months of 1981, 117 distinct wolf conflict areas (see Methods) could be identified throughout the Province (Tompa, this publication). In 47 (40%) conflict areas the problem was of a single isolated occurrence during the recording period; in 70 (60%) conflict areas a sequence of problems was reported, some lasting for only a month or less, others for a year or longer.

In 90 conflict areas the pack status of wolves could be identified: in 9 (10%) problems were caused by a single wolf; in 7 (8%) by more than one single or by pairs; and in 74 (82%) by packs. In 27 additional conflict areas the status of the wolves was uncertain, but packs were known to be present.

4.6. Demographic data

Information about pack size came from a variety of sources (e.g. track and sight reports by ranchers and investigating Ministry personnel), precluding accuracy, particularly outside the winter period. In 63 conflict areas where information was available, including the 7 areas with "pairs" but excluding the 9 areas with single wolves, the average size of problem packs was 5.9 animals. This estimate does not take into account wolves within the respective areas that were apparently not involved in conflict situations.

The sex was determined of 118 wolves taken through control: 74 (63%) were males and 44 (37%) were females. As most wolf carcasses were recovered during the late winter periods, when age determination under field conditions is difficult, pup/adult ratio was not determined.

4.7. Provincial problem wolf population

Wolf problems occurred in an average of 59 conflict areas annually, with a range of 54 to 62 (1978–80). Single wolves were involved in an average of 3 areas, and pairs and packs in an average of 47 areas per calendar year. In 9 areas the pack status of wolves was not known; assuming that it was similar to that in the 50 conflict areas where information on the pack status was available, an average of 326 wolves were in conflict situations annually within the

Province. This represents approximately 5% of the estimated provincial wolf population of 6300 (Tompa, this publication). The number of problem wolves estimated per year is probably realistic, because at least some ranchers would report observations in their areas.

4.8. Human contributing factors

Owners of domestic animals can inadvertently contribute to the development of wolf conflict situations. Letting dogs run wild may not only invite attacks by wolves, but may result in possible hybridization. Negligent animal husbandry that may result in serious local wolf–livestock conflicts includes (a) carcasses of livestock, dead from any causes, left on the range; (b) locating remote and uncontrolled calving and lambing grounds close to wolf areas; and (c) the prolonged absence of livestock surveillance on summer ranges. Although control of problem wolves is generally denied by the Ministry under such conditions, the developing problem may spread to neighbouring and otherwise faultless operations due to the conditioning of wolves to domestic prey. Furthermore, lack of surveillance not only prevents early problem recognition and prompt response, but also prevents adequate protection from other mortality factors. Animals missing on the range are often attributed to wolf predation once evidence of any other cause of death has vanished.

Wolf–livestock interaction has been studied recently by wildlife researchers in Canada and the United States to find the less obvious causal relationships. Hatler (1981, Fish and Wildl. Br., BC, unpubl. rep.) draws attention to malnutrition of stock, early turn-out on summer ranges following de-horning and castration, and the specific aggressiveness of cattle breeds as possible influences. He also refers to early turn-out date for newborn stock and calving on remote summer ranges as faulty practices and concludes that "...rather than considering such 'expected' calves as losses when they do not show up in the fall, they should be considered bonuses, if they do".

Fritts (1981, US Fish and Wildl., MN, unpubl. rep.) stresses the importance of a cattle pregnancy test before turn-out in the spring and observes that a strong prejudice among a few ranchers against wolves make then blame the wolf for losses that may be due to many other causes. Both Hatler and Fritts, as well as Bjorge (1980, Fish and Wildl. Div., Alta., unpubl. rep.) point to the importance of adequate surveillance of cattle on remote summer ranges and Bjorge correlates greater losses of stock on ranges with increasing vegetation cover.

More research is required to clarify the role of husbandry practices in wolf-related stock mortality, but it seems common sense to conclude on the basis of available information that preventive husbandry practices may go a long way toward reducing stock losses to wolves as well as to other mortality factors.

4.9. Dependence of wolves on domestic prey

Livestock killed by wolves annually (Table 1) weigh approximately 15 000 kg. Although Mech (1970) reports that wolves utilize 20–30% of domestic stock carcasses, we assume a 60% utilization to avoid any bias in the following calculation. The resulting 9000 kg domestic prey consumed by the calculated 326 problem wolves annually would provide 28 kg of meat per wolf. Based on the known consumption rates of wild wolves (Kolenosky 1972), this amount of meat would hardly support an active wolf for more than 10 days in a year.

Undoubtedly, scavenging of livestock dead from other causes could be an important factor for wolves during critical periods of food shortage. Nevertheless, the amount of food obtained by preying on domestic stock is considered to be inadequate to support resident wolf populations throughout the year. This suggests their primary dependence on wild prey.

5. Program evaluation and discussion

5.1. Action taken

Action to control wolves was taken in response to 286 (63%) of the 452 complaints received during 1978–80. In the 166 (37%) instances where control was not implemented it may have been unnecessary because action in response to other complaints from the same conflict areas had already been taken, the level of threat did not justify control, the absence of applicable methods and temporary work overload prevented action, or it may have been rejected because of faulty husbandry and the presence of livestock in areas of high wildlife uses, e.g. unattended stock in scrub areas. Preventive husbandry was recommended in response to 67 (15%) of the 452 complaints either in addition to or in place of wolf control; 33 of these recommendations were made during 1980, indicating the increased stress on non-lethal management, where practical.

5.2. Action results and method evaluation

Including 19 additional control actions in early 1981, 171 (56%) of 305 actions taken resulted in the killing of 455 wolves or 2.7 wolves per successful action. Strychnine and Compound 1080 baits were mainly used in control throughout 1978; shooting, primarily from helicopters, during a moratorium on poison baits (December 1978 – June 1980); and shooting, trapping, and individual 1080 baits from July 1980 to date (Tompa, this publication). The seasonal distribution of 380 wolves taken during 1978/80 is shown in Figure 5. The curves tend to follow the seasonal pattern of wolf complaints. The low number of wolves taken during the summer of 1979 and late spring of 1980 coincides with the moratorium and indicates the relative inapplicability of shooting during the snow-free period. Annual differences in the late winter peaks reflect changing snow and weather conditions, which affected the use of helicopters.

The carcasses of 140 (31%) of the 455 wolves were recovered. The death of the other 315 (69%) wolves was assumed, as the animals took poison baits, mainly 1080 preparations, or were wounded. A comparison of the effectiveness of various control methods (Table 3) fails to demonstrate a significant difference between shooting and trapping, and the use of 1080 baits in resolving local wolf problems lasting from 3 months to a year or longer.

5.3. Program effectiveness within conflict areas

In 31 (27%) of the 117 wolf conflict areas dispersed throughout the Province, wolf control activities were not implemented. In 10 of these control was refused because of faulty husbandry, unattended livestock in scrub areas, and for other reasons. In seven areas isolated harassment and dog-related complaints were not considered reasons for control. In 12 areas where livestock losses were verified the moratorium on poison baits prevented control. In two areas preventive husbandry was recommended in place of control. In addition, action to remove problem wolves failed in 18 (15%) conflict areas.

Problems did not last beyond a year in 39 (80%) of 49 conflict areas in which wolves were not removed through the official control program. In six areas problems occurred during 2 calendar years, in three areas during 3, and in one area during 4. Because of the apparently short duration of wolf conflict in other areas the lack of reliable information prevents evaluation. One may only speculate that in several areas a serious wolf conflict never in fact materialized.

In some areas problems might have been caused by transient animals or single problem wolves that perished for causes other than control. In other areas, particularly in those where, during the moratorium, the absence of practicable methods prevented wolf control, the lack of further complaints may indicate that dissatisfied ranchers stopped reporting and took control into their own hands. The illegal use of poison baits is suspected in several former conflict areas.

In 68 (52%) conflict areas, 171 control actions resulted in the killing of one or more wolves per action (Table 4). Within 27 (40%) of those areas, including all but 2 conflict areas where control was in response to problems caused by single wolves or pairs, wolf problems did not last beyond 1 calendar year. In one area, problems were caused through 4 calendar years by a series of singles which appeared sporadically on a group of neighbouring islands between Vancouver Island and the mainland. In the other area, only harassment reports were received through 3 consecutive years; one male was shot by the complainant in 1979 and a female in 1981. In the remaining 41 (60%) conflict areas with problems lasting beyond 1 year, pack involvement was identified or suspected.

Although the cumulative number of successful control actions within a conflict area increased with the number of years with local

Figure 5

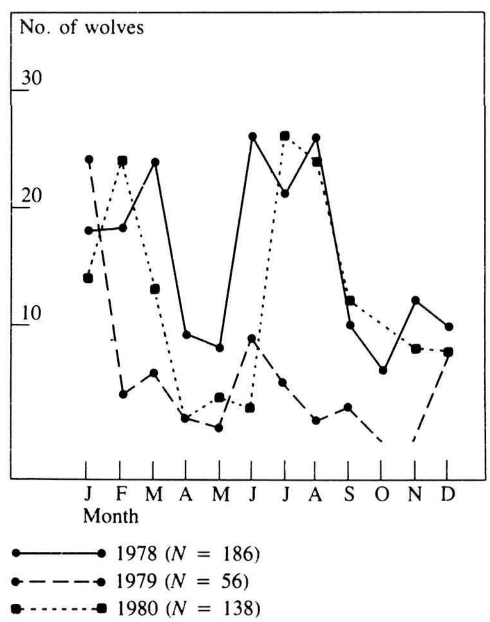


Figure 5
Seasonal distribution of wolves taken in livestock depredation control programs during three calendar years, 1978–80

Table 3
Relative effectiveness of wolf control, in relation to methods applied, lasting 3 months or more

	Effectiveness				
Control method	High	Moderate	Low	Nil	*N*
Strychnine baits	9	4	2	5	20
Compound 1080 baits	12	8	8	11	39
Shooting and trapping	14	8	7	12	41
Totals	35	20	17	28	100*

*Excludes four cases where action to remove wolves was a combination of the above control methods.

Table 4
Actions resulting in the removal of wolves between 1 January 1978 and 31 March 1981* in relation to complaint type and the number of years with wolf problems within individual conflict areas

	Wolf problems reported during									
	1 year		2 years		3 years		4 years		Totals	
	N	%	*N*	%	*N*	%	*N*	%	*N*	%
Conflict areas	27	40.0	18	27.0	16	23.0	7	10.0	68	100.0
Actions in response to:										
verified attacks	22	79.0	28	85.0	25	61.0	29	42.0	104	61.0
harassment	6	21.0	5	15.0	16	39.0	40	58.0	67	39.0
Totals	28	100.0	33	100.0	41	100.0	69	100.0	171	100.0
Annual action/area	1.0	–	0.9	–	0.9	–	2.5	–	–	–

*The eventual inclusion of additional action reports received during the remainder of 1981 is not expected to substantially alter the calculated ratios and percentages.

wolf problems, the average number of such actions stayed at one annually in all areas with problems in 1 to 3 calendar years. By contrast, there was an average of 2.5 control actions annually within the 7 areas with problems in all 4 years (Table 4).

Within the 45 conflict areas with wolf problems in 1 to 2 calendar years, the majority (79 and 85%) of 61 control actions were in response to wolves attacking livestock and domestic pets, in contrast to actions (21 and 15%) in response to harassment complaints. Control actions in response to harassment complaints increased to 39% in conflict areas with 3 years, and to 58% in areas with 4 years of complaints (Table 4).

One isolated case is of particular interest. Two adjacent packs shared a 15–20 km section of a river with overlapping range boundaries. The two areas were surrounded by forested mountain ranges. In one area, 42 wolves were killed in 12 control actions between March 1978 and February 1981 in response to 17 harassment and 6 livestock loss complaints. In the adjacent area, with livestock losses reported prior to 1978, 28 wolves were killed in response to 21 harassment reports between February 1978 and December 1980. In addition, one female that mauled a calf was shot by the complainant in 1979. In the absence of marked animals, and because of the broadly overlapping pack boundaries and the possibility of immigration, the pack relations of those wolves killed could not be determined with certainty. Of the 71 wolves reportedly killed 49 (69%) were removed during the winter season.

5.4. Discussion

The harassment complaints should be treated with caution, particularly in conflict areas where actual livestock kills and maulings are absent over prolonged periods. Control action in response to harassment reports is unavoidable in areas of confirmed livestock losses, because the wolves responsible may leave the site of the attack for a period, thereby preventing immediate action. It can also be expected that the continuous exposure of wolves to livestock will eventually lead to attacks. However, the presence of wolves in areas of mixed wildlife and agricultural uses does not necessarily present an immediate threat to livestock or other domestic animals. In 27 (40%) of the conflict areas in which wolves were killed, problems occurred in only 1 calendar year and in 18 (27%) areas through 2 years during the reporting period (Table 4).

The increasing number of harassment reports throughout the reporting period and their preponderance during late winter (January–March), suggests the possibility that these reports relate more to the visible presence of wolves close to human settlements and farm buildings than to actual wolf–livestock interaction.

The validity of control action in response to harassment reports is questionable, particularly in situations where such reports are not associated with concurrent wolf-related livestock losses. The constant removal of wolves not responsible for livestock depredation is unlikely to resolve the perceived "problem", as wolves will continue to be seen within the areas normally inhabited by them, causing repeated harassment complaints. By contrast, the successful killing of wolves that do attack livestock can be expected to resolve a local problem for a period, until wolves filling the vacuum through reproduction or immigration turn on the livestock.

Data comparison strongly supports the above assumption (Table 5); 41 (61%) of 67 wolf kills in response to harassment reports failed to resolve the "problem" within respective conflict areas. By contrast, only 29 (28%) of the 104 control actions in response to verified attacks failed to result in some level of program effectiveness ($P < 0.001$). The difference is particularly striking during the late winter period when most harassment reports are received. The problem-free period was also longer lasting following the control of wolves involved in attacks, indicating the gradual conditioning of new wolves to livestock. A similar delay in problem recurrence in relation to harassment reports is not obvious. The relatively high *initial* failure (22 of 66 or 33%) of control actions during April to December, in response to verified livestock losses, may relate to increased difficulty in removing all problem animals in one action during those seasons.

Table 5
Program effectiveness through wolf control in response to harassment reports and reports of verified livestock losses (January 1978 – March 1981)

Season	Subject of report		Effectiveness: High	Moderate	Low	Nil	*N*
January–March	Harassment	*N*	4	3	6	27	40
		%	10.0	7.5	15.0	67.5	
	Livestock loss	*N*	12	9	10	7	38
		%	32.0	24.0	26.0	18.0	
April–December	Harassment	*N*	5	5	3	14	27
		%	19.0	19.0	11.0	51.0	
	Livestock loss	*N*	23	13	8	22	66
		%	35.0	20.0	12.0	33.0	
Total	Harassment	*N*	9	8	9	41	67
		%	13.5	12.0	13.5	61.0	
	Livestock loss	*N*	35	22	18	29	104
		%	34.0	21.0	17.0	28.0	

6. Conclusions

The new strategy of reactive, site-specific management of problem wolves is supported by data that show that wolves within the Province do not present a general threat to human safety and livestock, but that problems are localized and limited. It is further indicated, although considerably more research information is required, that wolf-related livestock

Timber wolf feeding on Hereford calf, an example of the conflict between man and wolf that has a direct economic impact along the fringes of rural areas (photo: Tom Hall)

losses may be effectively reduced in some situations by preventive husbandry practices alone or in combination with control action.

Notwithstanding seasonal and local applicability, all control methods employed following verified attacks during the reporting period were equally effective in resolving conflicts with wolves, whether control was directed at problem individuals or packs. Therefore the on-site investigation of reported wolf complaints as well as prompt follow-up action seem to be of critical importance in increasing program effectiveness.

Although action in response to harassment reports can be justified in areas of concurrent wolf-related livestock losses, particularly where previous control action to remove problem wolves had been unsuccessful, action should eventually cease until new attacks on livestock within a particular area are confirmed.

The possibility exists that the constant removal of wolves not responsible for livestock depredation may actually lead to local livestock losses due to changes caused in the local wolf population. Such constant disruption of population regulatory mechanisms can in itself result in local population increases through reproduction or immigration. However, this aspect of wolf–livestock interaction is little understood at the moment and needs further research.

It is safe to conclude that the present control program does not threaten the status of the wolf within British Columbia. Restriction of control methods at public demand does not necessarily benefit the wolf. During the moratorium on poison baits, communication was broken with many ranchers, who are now suspected of controlling wolves within their area by legal as well as illegal means. Such uncontrolled action may harm the wolf as well as other species. Public education is therefore an important part of future management programs. A thorough understanding by the interested public, as well as by potential complainants, of the extent and causal relationships of wolf conflicts and the nature and impact of management methods will assist a balanced program. This, in the long run, will benefit the public, the producers, and the wolf.

7. Acknowledgements

The assistance of all my colleagues who provided information and comments is gratefully acknowledged. I particularly thank J.P. Thornton for his help in data evaluation, and L. Wells for the preparation of figures. I am also thankful to my supervisor, D.R. Halladay, for allowing time for the preparation of the paper. The help of my wife, Christel, is also appreciated. The typing of this report was cheerfully done by Lynda Adams.

A method to aid in discrimination of tracks from wolves and dogs

Wolf tracks: *top*, front and hind paws of a pup superimposed; *centre*, front paw of an adult; *bottom*, hind paw of an adult (photo: L.N. Carbyn)

Richard B. Harris
Robert R. Ream

1. Abstract

A study was conducted in an attempt to provide a method to distinguish between wolf and dog tracks. Plaster casts were made from 72 dog and 35 wolve tracks. Variation among dogs was great, therefore six common large breeds were sampled.

Dog tracks are indistinguishable from wolf tracks on the basis of size alone. However, parameters of shape (ratios) are homogeneous within dog-breed tracks and also within wolf tracks from disparate geographic areas. Seven wolf track ratios are significantly different from the corresponding ratio of at least one breed of dog. These seven shape ratios are used in discriminant function analysis, which places an individual track along a linear decision scale. Application of the discriminant function method to an unknown track is discussed.

Zones of rejection along the scale are not identified and probability of error cannot be determined, but the midpoint serves as the best available discriminator. This method aids wolf–dog track discrimination but should not constitute the sole basis for field differentiation of wolves and dogs.

2. Introduction

Researchers documenting the presence of wolves (*Canis lupus*) in areas where they are very rare or newly re-established face the initial problem of locating the animals. US Federal land management agencies also require accurate information on wolf distribution because the US Endangered Species Act requires federal actions to consider impacts on the Northern Rocky Mountain Wolf (*C. l. irremotus*).

In forested areas, where sightings are rare, tracks are an important indicator of wolf presence and activity. Domestic dogs, with or without humans, are sometimes seen in areas occupied by wolves. Discrimination between wolf and dog tracks has been limited to subjective accounts (Iljin 1941; Young and Goldman 1944; Murie 1954; Mech, pers. comm.) and has been a serious problem encountered during field work of the Wolf Ecology Project, University of Montana (Ream and Mattson, in prep.).

Accurate wolf–dog track discrimination is desirable both from a research perspective, to minimize time and energy spent on erroneous reports, and from a management standpoint, to aid in defining distribution in areas were wolves are rare. This study reports on the feasibility of distinguishing wolf tracks from dog tracks, using discriminant function analysis.

3. Methods

We made plaster casts of tracks of front feet from 72 dogs and 35 wolves using regular casting plaster. We chose front feet in preference to hind because the front heel pad often registers more clearly (Murie 1954). All dogs were walked through the same wooden box containing river-bottom sand to reduce variation caused by differing substrates. Although this procedure could not be followed for wolves, we discarded distorted or indistinct casts, ending up with 32 usable ones. These comprised: 3 from northeast Minnesota; 6 from the Kenai Peninsula, Alaska; 16 from a captive pack in Halifax, Nova Scotia; and 7 from northeast Alaska from the collection of Olaus Murie.

Seven ratios that included 11 measurements were found to be useful. Five additional measurements and 10 ratios were computed, but were not found to be valuable discriminates. Measurements were made to the nearest millimetre using calipers.

Very little homogeneity exists among dogs as a species although much exists within breeds. Thus comparisons were made on a breed-by-breed basis. We sampled purebred adult dogs, both males and females, from western Montana, selecting larger breeds and larger individuals within each breed. We studied six common large breeds (American Kennel Club 1975): Alaskan malamute, bloodhound, great Dane, German shepherd, Irish wolfhound, and St. Bernard. The tracks of four smaller common breeds (Siberian husky, golden retriever, collie, and Labrador retriever) were found to resemble those of wolves in size only very rarely and were not subjected to statistical analyses.

We used standard two sample t-tests to determine for which parameters population groups differed, and Mann-Whitney tests to determine whether males and females differed within each dog breed. Discriminant function analysis was found to be the most useful statistical method for separating two similar populations (Freese 1967, Conner and Adkisson 1976). We used three ratios in each test, although they were not necessarily the same in

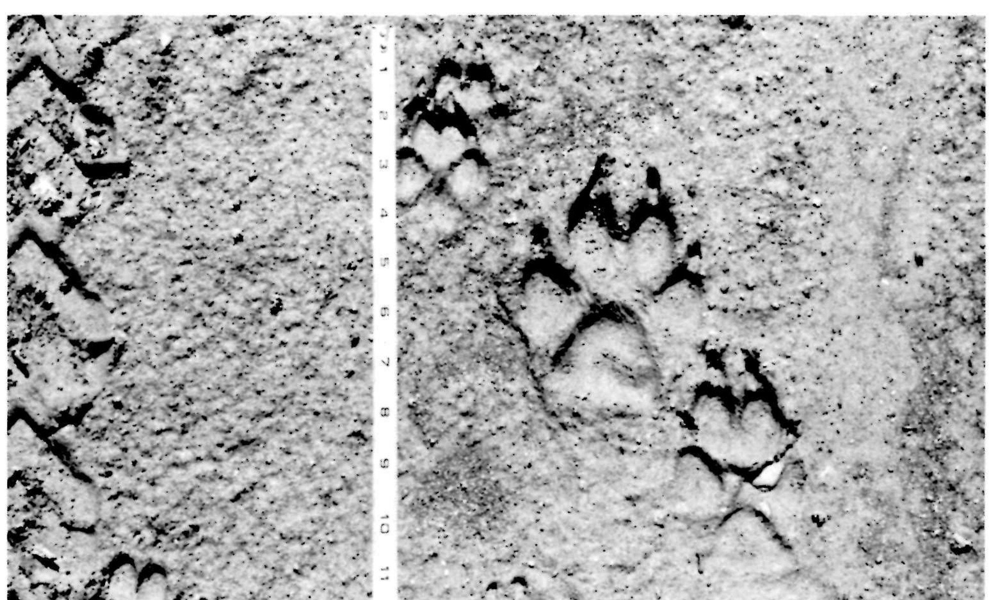
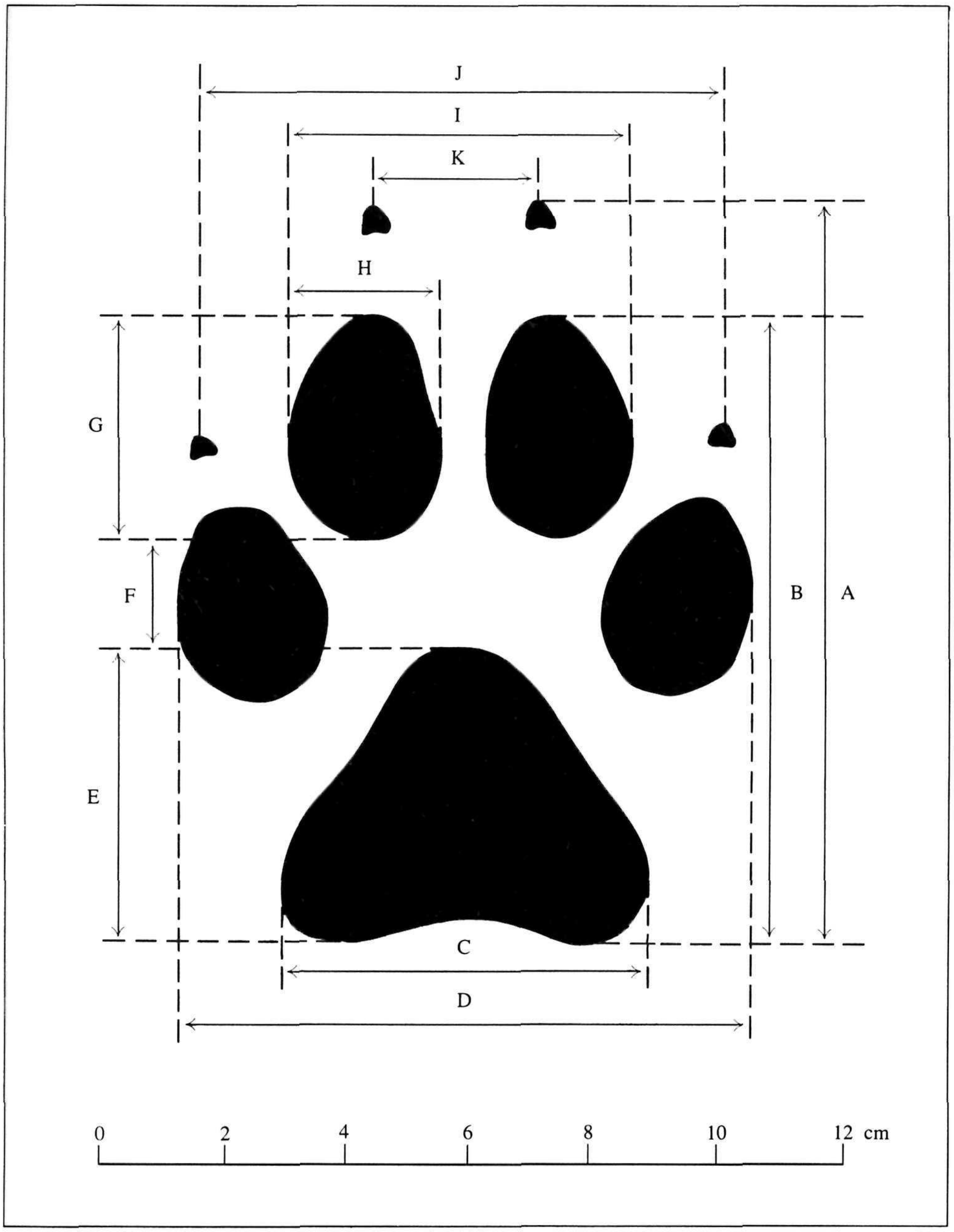


Figure 1
Track measurements used for ratio computations (not full size)

Figure 1



Ratios

1	E/A	**5**	K/I
2	E/C	**6**	F/B
3	C/J	**7**	$\frac{G \times H}{E \times C}$
4	J/D		

each case. The ratios were chosen for their discriminating effectiveness between the two groups tested. Computations were performed by the BMD 04 computer program developed by the UCLA Medical School and executed on the DEC 20 University of Montana computer.

4. Results

4.1. Size

We found size to be ineffective for wolf–dog track discrimination. Our wolf samples varied from 104 to 137 mm in total length ('A' in Fig. 1) with a mean of 116.7 mm. Wolf tracks from Minnesota were smaller ($\bar{X}$ = 106 mm) than those from Alaska ($\bar{X}$ = 123 mm), which is consistent with the differences in overall body size of wolves from those areas (Young and Goldman 1944). Our largest dog breed, St. Bernard, had a mean total length of 118.2 mm, with a maximum of 129 mm. Even among medium large breeds, a few tracks resembled those of wolves.

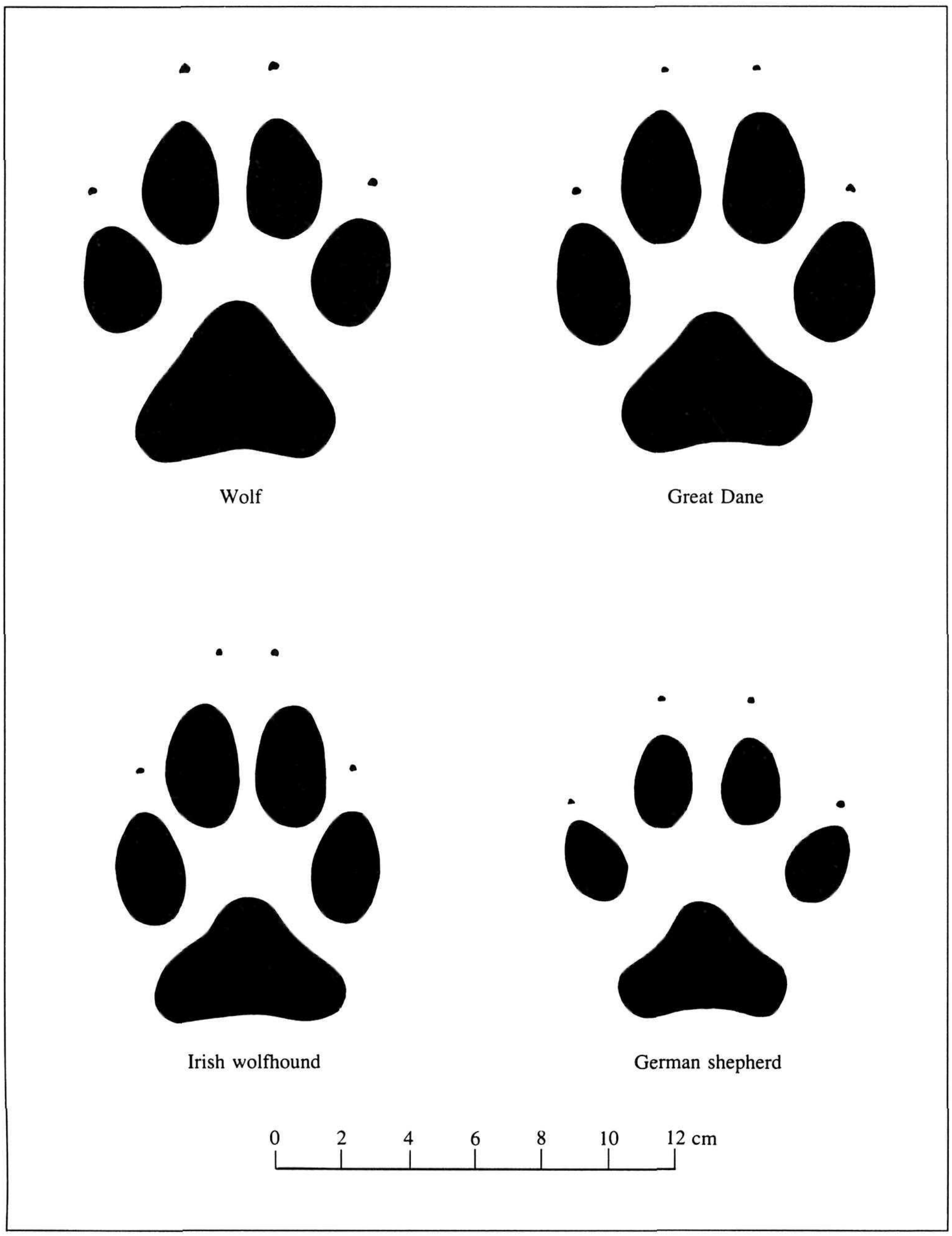
Among breeds sampled we found that 110 mm is a useful dividing line between the largest breeds (great Dane, St. Bernard, and Irish wolfhound) and the medium-large breeds (German shepherd, Alaskan malamute, and bloodhound). Male dog tracks were slightly larger than female tracks.

4.2. Shape

Although considerable geographic variation exists in the size of wolf tracks we found relatively little variation in shape. None of our wolf sub-groups differed significantly from each other. Parameters of track shape were determined by using ratios of measurements. Figure 1 shows the 11 measurements used to compute the seven ratios used in the discriminant function analysis. Table 1 lists the shape parameters, their mean ratios, and corresponding probability values. Figure 2 graphically illustrates tracks of a wolf and three breeds of dog, using the seven mean ratios in each case. The shape of the dog track did not differ between sexes.

Figure 2
Wolf and dog tracks based on mean measurements of each (not full size)

Figure 2



4.3. Discriminant function analysis

This method emphasizes differences in populations by selecting the best discriminates and weighting them according to their relative importance by means of coefficients. A group mean is produced that can be placed on a linear decision scale (Table 2).

For all groups sampled, confidence intervals based on the group mean for an individual track overlap considerably because of large standard deviations. Identification of a zone of rejection for one group along the linear scale would also reject an unacceptably high proportion of the opposing group. Thus, the scale midpoints are viewed as reference points only and do not denote that the values to the left are exclusively dog or that the values to the right are exclusively wolf. The probability of incorrectly classifying an individual track cannot be deduced from the decision scale. The midpoints do serve, however, as the best available indicator of the relative probability of an individual track belonging to one group or the other.

4.4. Application of method

The discriminant function method is used in the following way. The 11 measurements (Fig. 1) are taken from a plaster cast of the unknown track. Care must be taken that it is not a hind foot track (see Murie 1954, for discussion of hind foot – front foot differentiation). From these measurements the seven ratios shown in Figure 1 are calculated. The three ratios for each test are multiplied by their appropriate coefficients (both listed in Table 2). The products are then summed and the resulting number is plotted on a linear scale. Its position on the scale when compared with the wolf mean, dog-breed mean, and midpoint indicates its probability of being a wolf or the specific dog breed.

This test must be repeated for all six dog breeds unless the track is over 110 mm in total length, in which case only St. Bernard, great Dane, and Irish wolfhound should be tested. Values of "wolf" may occur on one or more of the tests, even if the track is actually that of one of the dogs tested. For example, if the track is actually that of a great Dane, in the

Table 1
Seven mean footprint ratios (see Fig. 1 for measurements) and associated *t*-test* significance by wolf and six dog breeds

Discriminant function variable number	Ratio	Wolves $N = 32$	St. Bernards $N = 9$	Great Danes $N = 11$	Irish wolfhounds $N = 6$	Blood-hounds $N = 9$	Alaskan malamutes $N = 11$	German sheperds $N = 13$
1	E/A	40.88	33.29†	36.80	33.67†	39.78	39.45	38.09
2	E/C	80.91	68.00†	74.22‡§	67.20‡§	75.56	75.73‡§	72.73†
3	C/J	70.64	68.51	66.00	82.67	74.22	67.10	59.70†
4	J/D	89.45	91.12	88.00	86.20	86.44	94.10	96.10‡§
5	K/I	49.40	43.37	47.00	33.50‡§	48.75	54.00	56.11
6	F/B	17.61	20.70	17.86	24.20‡§	24.74	19.71	26.82†
7	$\frac{G \times H}{E \times C}$	29.82	41.73†	42.60†	38.26†	35.10	32.00	30.30

*Two sample *t*-tests were performed between wolf means and each of the six dog breed means for each of the seven ratios. All ratios multiplied by 100.
†Significant at $P \leq 0.001$.
‡Significant at $P \leq 0.01$.
§Significant at $P \leq 0.05$.

Table 2
Linear decision scales for six breeds of dog showing group means and midpoints

Variable	Co-efficients*	Dog breed	Midpoint	Wolves
2	−0.17551	$\bar{X} = -0.22332$	−0.27263	$\bar{X} = -0.32195$
3	−0.37572			
6	−0.48173	German shepherds		
2	−0.23093	$\bar{X} = -0.11815$	−0.10437	$\bar{X} = -0.09059$
4	−0.28943			
5	−0.03815	Alaskan malamutes		
2	−0.06426	$\bar{X} = -0.35131$	−0.31908	$\bar{X} = -0.28686$
6	−0.65239			
7	−0.39768	Bloodhounds		
2	−0.46767	$\bar{X} = -0.16786$	−0.29513	$\bar{X} = -0.42240$
5	−0.68867			
7	−0.98935	Irish wolfhounds		
1	−0.17450	$\bar{X} = -0.30581$	−0.23068	$\bar{X} = -0.15555$
2	−0.11753			
7	−1.07333	Great Danes		
1	−1.62743	$\bar{X} = -0.12969$	−0.00458	$\bar{X} = -0.13886$
2	−0.15743			
7	−1.35790	St. Bernards		

*Determined by BMD 04 Discriminant Function Analysis Program.

"wolf vs. German shepherd" test the answer must necessarily be incorrect as the track is neither. Often the result in this case will be on the "wolf" side of the midpoint, as values of ratios for great Danes may be closer to those of wolves than to those of German shepherds. Thus a value on the "wolf" side of the midpoint on an individual test could easily mislead the investigator. For this reason, only if all six results show values close to "wolf" (or all three results if the track is over 110 mm total length) should the test be considered positive for wolf. On the other hand, any results close to the dog breed in question should cause the investigator to reject wolf classification.

5. Discussion

Two-group discriminant function analysis emphasizes and quantifies differences between wolf tracks and dog tracks. Probability values cannot be assigned to the results, but midpoints along linear decision scales serve as the best available discriminators. This method should not be used in isolation, but should complement other relevant information such as *length of stride* (Murie 1954); *direction of stride* — dogs tend to waver along a path much more than wolves, according to Burt and Grossenheider (1952); proximity to people; likelihood of wolves being in the area; nearby scats, which Weaver and Fritts (1979) suggest can be distinguished from coyote scats at 30 mm diameter; or kills. O'Gara (1978) describes characteristics of dog kills.

The study dealt with only six breeds of dog. We feel that these six constitute the most common breeds leaving tracks likely to be confused with wolf tracks, but other dogs, both purebred and mongrel, could be complicating factors. We tested a few tracks of other breeds to see if our method could be used to identify their tracks. Although sample sizes were small, golden retrievers, collies, and mongrel sled dogs all showed values close to those of German shepherds and Alaskan malamutes; mastiffs and akitas all showed values close to great Danes and St. Bernards. Thus it appears that even dog tracks of breeds untreated in this study would not be incorrectly classified as wolf tracks.

A major limitation of this method is that our study sample was restricted to undistorted tracks made in wet river bottom sand. We made no attempt to quantify the variation inherent in different substrates (melting snow, for example) or slopes. Results obtained by using distorted tracks or other substrates may therefore not be valid. The investigator is left with the responsibility of integrating the results of this method with other available data.

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Appendix 1

Summary of the status of wolves in Saskatchewan

E. Wiltse

1. Distribution

Approximately northern two-thirds of the province. Prince Albert National Park is within the southern boundary of the current distribution.

2. Legal status

Identified as "fur animals" under The Wildlife Act. Harvests are regulated by restricting trapping from 15 October to 15 March.

3. Economic status

Economic importance as a furbearer (Table 1) is insignificant. Approximately 1283 wolves were harvested over a 5-year period (1975–80) for a total cash value of approximately $126 183.

4. Predator control

Control programs were carried out annually from mid 1930s to 1975–76. Since then control has been area-specific. Poison baits are used to a limited extent where wolf–livestock depredation problems occur along fringe agricultural–forest zones. Although wolves are not now being controlled as part of game management, in circumstances where low ungulate populations exist and where wolves are considered to be influencing recovery rates, control measures may be implemented.

5. Areas of total protection

Prince Albert National Park, 3875 km^2.

Table 1
Economic importance of wolves in Saskatchewan

Trapping period	No. of pelts	Value ($)	Average price ($)
1975–76	366	29 434	80
1976–77	265	23 373	88
1977–78	155	12 883	83
1978–79	262	32 530	124
1979–80	235	27 963	119
Total	1283	126 183	
Annual average	257	25 346	98

Appendix 2

Summary of the status of wolves in Newfoundland and Labrador

Stuart Luttich

1. Distribution

Wolves were exterminated on the island of Newfoundland in the early 1900s; the last known specimen was taken in 1911 (Tuck, L.M., Newfoundland Quart. 75(3):21–56). Wolves are currently common throughout Labrador. Wolves in southern Labrador are thought to be smaller and darker than those farther north.

2. Historical presence

During the first half of the 20th century wolves were uncommon in Labrador. Wolf pelts were rarely reported in the Hudson's Bay Company fur harvest and records, and received little mention in the Company's post journals. Trappers report never having killed or even observed a wolf until the late 1950s. The absence of wolves is correlated with the disappearance of caribou from northern Labrador and Ungava between 1890 and 1910. After 1950, caribou began a period of unprecedented recovery and moose have moved into the area in recent years.

3. Legal status

The wolf is classified as a furbearer. The species is protected during the breeding season. No predator control programs are carried out.

Literature cited

Allen, D.L. 1979. Wolves of the Minong, their vital role in a wild community. Houghton Mifflin, Boston, MA. 499 pp.

Altmann, D. 1974. Beziehungen zwischen sozialer Rangordnung und Jungenaufzucht bei *Canis lupus*. Zool. Garten. N.F. Jena 44:235–236.

American Kennel Club. 1975. The complete dog book. Howell Book House, New York, NY. 580 pp.

Anon. 1967. USF&WS Div. of Wildl. Serv., Policy handb. Washington, DC.

Anon. 1972. Predator Control 1971, Rep. to the Council on Environ. Quality and Dep. of the Inter. by the Advis. Comm. on Predator Control. Counc. on Environ. Quality and US Dep. Inter., Washington, DC. 206 pp.

Anon. 1979. Mammalian predator damage management for livestock protection in the western United States. Final Environ. Impact Statement. Dep. Inter., Washington, DC. 787 pp.

Bailey, T.N. 1978. Moose populations on the Kenai National Moose Range. Proc. N. Am. Moose Conf. Workshop 14:1–20.

Bailey, T.N.; Bangs, E.E. 1980. Moose calving areas and use on the Kenai National Moose Range, Alaska. Proc. N. Am. Moose Conf. Workshop. pp. 289–313.

Baker, M.C.; Marler, P. 1980. Behavioral adaptations that constrain the gene pool in vertebrates. Pages 59–80 *in* Markl, H., ed. Evolution of social behavior: hypotheses and empirical tests. Verlag Chemie, Deerfield Beach, FL.

Ballantyne, E.E. 1958. Rabies control in Alberta wildlife. Vet. Med. pp. 87–91.

Ballantyne, E.E.; O'Donoghue, J.G. 1954. Rabies control in Alberta. J. Am. Vet. Assoc. 125:316–326.

Ballard, W.B.; Spraker, T.H.; Taylor, K.P. 1981. Causes of neonatal moose calf mortality in south central Alaska. J. Wildl. Manage. 45:335–342.

Banfield, A.W.F. 1974. The mammals of Canada. Univ. of Toronto Press, Toronto, Ont. 438 pp.

Banfield, A.W.F. 1954. Preliminary investigations of the barren-ground caribou. Can. Wildl. Serv., Wildl. Manage. Bull. Ser. 1, No. 10A and 10B. 79 pp.

Banville, D. 1979. Quelques aspects de l'écologie et de la dynamique de population du loup (*Canis lupus*) dans l'Outaouais. Thèse de maîtrise, dép. de Biologie, univ. Laval, Ste-Foy, Qué. 64 pp.

Banville, D. 1981. Bilan du contrôle des prédateurs au Québec de 1905 à 1980. Ministère québécois du Loisir, de la Chasse et de la Pêche, Dir. recherche faunique. Rapport spécial n° 15. 54 pp.

Bartlett, G.W. 1909. How shall we destroy the wolves? Rod and Gun, Vol. 11, No. 3 (Aug. 1909):240–242.

Bateson, P.P.G. 1978. Sexual imprinting and optimal outbreeding. Nature 273:659–660.

Bateson, P.P.G. 1979. How do sensitive periods arise and what are they for? Anim. Behav. 27:470–481.

Belt, C.B. 1956. History of the committee on conservation of forests and wildlife of the Camp Fire Club of America, 1901–1956. Camp Fire Club of America, New York, NY. 76 pp.

Bergerud, A.T. 1974. Decline of caribou in North America following settlement. J. Wildl. Manage. 38:757–770.

Bergerud, A.T. 1979. A review of the population dynamics of caribou and wild reindeer in North America. Pages 556–581 *in* Reimers, E.; Gaara, E.; Skjenneberg, S., eds. Proc. 2nd Int. Reindeer/Caribou Symp. Directoret for vilt og Ferskvannsfisk, Trondheim, Norway. 799 pp.

Berryman, J.H. 1972. The principles of predator control. J. Wildl. Manage. 36(2):395–400.

Bibikov, D.I. 1975. The wolf in the USSR. Pages 29–35 in Pimlott, D.H., ed. Proc. 1st Working Meet. of Wolf Specialists and 1st Int. Conf. on Conserv. of the Wolf. IUCN, Morges, Switzerland. 145 pp.

Bjorge, R.R. 1980. Management and research of the wolf–livestock conflict in Alberta. Pages 72–76 *in* Proc. 27th Annu. Meet. Can. Pest Manage. Soc., Edmonton, Alta.

Blood, D.A. 1974. Variation in reproduction and productivity of an enclosed herd of moose (*Alces alces*). Proc. Int. Congr. Game Biol. 11:59–66.

Boitani, L.; Zimen, E. 1975. Status of the wolf in Italy. Pages 73–78 *in* Pimlott, D.H., ed. Proc. 1st Working Meet. of Wolf Specialists and 1st Int. Conf. on Conserv. of the Wolf. IUCN, Morges, Switzerland. 145 pp.

Bojovic, D.; Colic, D. 1975. Wolves in Yugoslavia. Pages 53–61 *in* Pimlott, D.H., ed. Proc. 1st Working Meet. of Wolf Specialists and 1st Int. Conf. on Conserv. of the Wolf. IUCN, Morges, Switzerland. 145 pp.

Bos, G.N. 1975. A partial analysis of the current population status of the Nelchina Caribou Herd. Pages 170–180 *in* Luick, J.R., ed. Proc. 1st Int. Reindeer/Caribou Symp. Biol. Pap. Univ. of Alaska. Spec. Rep. No. 1.

Burkholder, B.L. 1959. Movements and behavior of a wolf pack in Alaska. J. Wildl. Manage. 23:1–11.

Burpee, J. (Ed.). 1907. York factory to the Blackfeet country: the journal of Anthony Hendry, 1754–55. Proc. and Trans. Roy. Soc. Can. Ser. 3, Vol. 1. pp. 307–354.

Burt, W.; Grossenheider, R. 1952. A field guide to mammals. Houghton Mifflin Co., Boston, MA. 289 pp.

Bush, G.L. 1975. Modes of animal speciation. Pages 339–364 *in* Johnston, R.F.; Frank, P.W.; Michener, C.D., eds. Annual review of ecology and systematics. Vol. 6. Annual Reviews Inc., Palo Alto, CA.

Cahalane, V.H. 1946. Shall we save the larger carnivores? The Living Wilderness 17:17–22.

Callison, I.P. 1948. Wolf predation in the north country. I.P. Callison, Seattle, Washington, DC. 89 pp.

Carbyn, L.N. 1974. Wolf population fluctuations in Jasper National Park, Alberta. Biol. Conserv. 6:94–101.

Carbyn, L.N. 1975*a*. Wolf predation and behavioural interactions with elk and other ungulates in an area of high prey density. Ph.D. Thesis, Univ. of Toronto, Toronto, Ont. Can. Wildl. Serv. rep. 1974. 234 pp.

Carbyn, L.N. 1975*b*. Factors influencing activity patterns of ungulates at mineral licks. Can. J. Zool. 53: 377–384.

Carbyn, L.N. 1981. Territory displacement in a wolf population with abundant prey. J. Mammal. 62:193–195.

Carbyn, L.N. 1982*a*. Incidence of disease and its potential role in the population dynamics of wolves in Riding Mountain National Park, Manitoba. Pages 106–116 *in* Harrington, F.; Paquet, P., eds. Wolves of the world: perspectives of behavior, ecology, and conservation. Noyes Publications, Park Ridge, NJ. 474 pp.

Carbyn, L.N. 1982*b*. Coyote population fluctuations and spatial distribution in relation to wolf territories in Riding Mountain National Park, Manitoba. Can.-Field Nat. 96:176–182.

Carbyn, L.N. In press. Wolf predation on elk in Riding Mountain National Park, Manitoba. J. Wildl. Manage. Vol. 47.

Caughley, G. 1977. Analysis of vertebrate populations. Wiley, New York, NY. 234 pp.

Chapman, R.C. 1978. Rabies: decimation of a wolf pack in Arctic Alaska. Science 201:365–367.

Christian, J.J. 1978. Neurobehavioral and endocrine regulation of small mammal populations. Pages 143–158 *in* Snyder, D.P., ed. Populations of small mammals under natural conditions. Univ. of Pittsburgh Press, Pittsburgh, PA.

Christie, D.W.; Bailey, J.B.; Bell, E.T. 1972. Classification of cell types in vaginal smears during the canine oestrous cycle. Brit. Vet. J. 128:301–310.

Clark, K.R.F. 1971. Food habits and behavior of the tundra wolf on central Baffin Island. Ph.D. Thesis, Univ. of Toronto, Toronto, Ont. 223 pp.

Clarke, C.D.H. 1940. A biological investigation of the Thelon Game Sanctuary. Natl. Mus. Can. Bull. 96, Biol. Ser. 25.

Clarke, C.H.D. 1970. Wolf management in Ontario. Pages 19–23 *in* Jorgensen, S.E.; Faulkner, C.E.; Mech, D.L., eds. Symp. on Wolf Management in Selected Areas of North America. 35th N. Am. Wildl. and Nat. Resour. Conf., Chicago, IL. 50 pp.

Coady, J. 1976*a*. Interior moose — why the decline? Alaska Fish Tales and Game Trails 9:12–14. Alaska Dep. of Fish and Game, Juneau, AK.

Coady, J. 1976*b*. Status of moose populations in interior Alaska. Alaska Dep. of Fish and Game, Wildl. Leaflet No. 2.

Concannon, P.W.; Hansel, W.; Visek, W.J. 1975. The ovarian cycle of the bitch: plasma estrogen, LH, and progesterone. Biol. of Reprod. 112–121.

Conner, R.; Adkisson, C. 1976. Discriminant function analysis: a possible aid in determining the impact of forest management on woodpecker nesting habitat. Forest Sci. 22:122-127.

Cook, F.W. 1945. White-tailed deer in the Great Plains region. J. Wildl. Manage. 9:237–242.

Coues, E. 1897. New light on the early history of the greater northwest. The manuscript journals of Alexander Henry and David Thompson, 1799–1814. Vol. 2. Francis P. Harper, New York, NY. pp. 632–746.

Cowan, I. McT. 1947. The timber wolf in the Rocky Mountain National Parks of Canada. Can. J. Res. 25:139–174.

Cowan, I. McT. 1954. The occurrence of the Pleistocene wolf *Canis dirus* in the Rocky Mountains of central Alberta. Can. Field-Nat. 68:44.

Cowan, I. McT.; Guiguet, C.J. 1965. The mammals of British Columbia. B.C. Prov. Mus., Handbook No. 11., Victoria, B.C. 414 pp.

Crête, M.; Taylor, R.J.; Jordan, P.A. 1981. Optimization of moose harvest in southwestern Québec. J. Wildl. Manage. 45:598–611.

Crisler, L. 1956. Observations of wolves hunting caribou. J. Mammal. 37:337–346.

Crisler, L. 1958. Arctic Wild. Harper, New York, NY. 301 pp.

Cross, E.C. 1937. Wolf! Wolf! Rod and gun in Canada. 38:18, 32.

Crow, J.F.; Kimura, M. 1970. An introduction to population genetics theory. Harper and Row, New York, NY. 591 pp.

Cumming, H.G.; Walden, F.A. 1970. The white-tailed deer in Ontario. Ont. Dep. Lands and Forests. Spec. publn. 24 pp.

Davies, N.B. 1978. Ecological questions about territorial behaviour. Pages 317–350 *in* Krebs, J.R.; Davies, N.B., eds. Behavioural ecology: an evolutionary approach. Sinauer Assoc., Sunderland, MA. 494 pp.

Davies, J.L.; Franzmann, A.W. 1979. Fire–moose–caribou interrelationships. Proc. N. Am. Moose Conf. Workshop 15:80–118.

Dawkins, R.; Krebs, J.R. 1978. Animal signals: information or manipulation? Pages 282–309 in Krebs, J.R.; Davies, N.B., eds. Behavioural ecology: an evolutionary approach. Sinauer Assoc., Sunderland, MA. 494 pp.

Doerr, J. 1979. Population analysis and modeling of the Western Arctic Caribou Herd with comparisons to other Alaskan *Rangifer* populations. M.S. Thesis, Univ. of Alaska, Fairbanks, AK. 341 pp.

Douglas, C.W. 1964. The program to manage deer is underway. Ont. Fish and Wildl. Rev. 2:3–11.

Eberhardt, L. 1960. Estimation of vital characteristics of Michigan deer herds. Michigan Dep. Conserv. Game Div. Rep. no. 2282. 192 pp.

Errington, P.L. 1946. Predation and vertebrate populations. Quart. Rev. Biol. 21:144–177, 221–245.

Fentress, J.C.; Ryon, C.J. 1982. A long term study of distributed pup feeding and associated behavior in wolves. Pages 238–261 *in* Harrington, F.H.; Paquet, P.C., eds. Wolves of the world: perspectives on behavior, ecology, and conservation. Noyes Publications, Park Ridge, NJ. 474 pp.

Fox, M.W. 1971. Socio–infantile and socio–sexual signals in canids: a comparative and ontogenetic study. Zeits. für Tierpsych. 28:185–210.

Francis, G. 1960. Observations of some carnivores by wardens in the mountain National Parks of Canada. Can. Field-Nat. 74:158–160.

Franklin, I.R. 1980. Evolutionary change in small populations. Pages 135–149 *in* Soule, M.E.; Wilcox, B.A., eds. Conservation biology. Sinauer Assoc., Sunderland, MA. 395 pp.

Franzmann, A.W.; Schwartz, C.C.; Peterson, R.O. 1980. Moose calf mortality in summer on the Kenai Peninsula, AK. J. Wildl. Manage. 44(3):764–768.

Freeman, M.M.R. 1976. Inuit land use and occupancy project. Vol. 1. Land use and occupancy. Dep. of Indian and Northern Affairs. INA Publ. No. QS8054-001-EE-A1. 263 pp.

Freese, F. 1967. Elementary statistical methods for foresters. USDA For. Serv., US Gov. Printing Office. 87 pp.

Fritts, S.H.; Mech, L.D. 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. Wildl. Monogr. 80. 79 pp.

Fuller, T.K.; Keith, L.B. 1980. Wolf population dynamics and prey relationships in northeastern Alberta. J. Wildl. Manage. 44:583–602.

Fuller, W.A. 1962. The biology and management of the bison of Wood Buffalo National Park. Can. Wildl. Serv. Wildl. Manage. Bull. Ser. 1. 52 pp.

Fuller, W.A.; Novakowski, N.S. 1955. Wolf control operations, Wood Buffalo National Park, 1951–52. Can. Wildl. Serv. Wildl. Manage. Bull. Ser. 1, No. 11.

Geist, V. 1968. On delayed social and physical maturation in mountain sheep. Can. J. Zool. 46:899–904.

Georges, S. 1976. A range extension of the coyote in Québec. Can. Field-Nat. 90(1):78–79.

Goldman, E.A. 1944. The wolves of North America. Pt. II. Pages 398–636 *in* Classification of wolves. Am. Wildl. Inst., Washington, DC. 636 pp.

Gray, A.P. 1972. Mammalian hybrids: a check-list with bibliography. Commonw. Agric. Bureaux, Slough, England. 262 pp.

Green, H.U. 1951. The wolves of Banff National Park. Can. Dep. Resour. Dev., Natl. Parks Br., Can. Natl. Parks and Hist. Sites Serv. Rep. 47 pp.

Greenwood, P.J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. Anim. Behav. 28:1140–1162.

Gunson, J.R.; Dies, K.H. 1980. Sylvatic trichinosis in Alberta. J. Wildl. Dis. 16:525–528.

Gunson, J.R.; Nowak, R.M. 1979. Largest gray wolf skulls found in Alberta. Can. Field-Nat. 93:308–309.

Gurba, J.B.; Neave, D.J. 1979. Problem wildlife management. Alberta Agric. and Alberta Energy and Nat. Resour. Rep. 24 pp.

Haber, G.C. 1974. Wolves and the endangered species concept — a different view. Pages 110–119 *in* Proc. Symp. on Endangered and Threatened Species of North America. June 11–14, 1974. Washington, DC.

Haber, G.C. 1977. Socio-ecological dynamics of wolves and prey in a subarctic ecosystem. Ph.D. Thesis, Univ. of British Columbia, Vancouver, B.C. 785 pp.

Haber, G.C.; Walters, C.J.; Cowan, I. McT. 1976. Stability properties of a wolf–ungulate system in Alaska and management implications. Inst. Resour. Ecol. and Dep. Zool., Univ. of British Columbia, B.C. Publ. R-5-R. 104 pp.

Haglund, B. 1975. The wolf in Fennoscandia. Pages 36–43 *in* Pimlott, D.H., ed. Proc. 1st Working Meet. of Wolf Specialists and 1st Int. Conf. on Conserv. of the Wolf. IUCN, Morges, Switzerland. 144 pp.

Hall, A.M. 1971. Ecology of beaver and selection of prey by wolves in central Ontario. M.Sc. Thesis. Univ. of Toronto, Toronto, Ont. 116 pp.

Hall, E.R. 1981. The mammals of North America. 2 vols. John Wiley and Sons, New York, NY. 1181 pp.

Hall, E.R.; Kelson, K.R. 1959. The mammals of North America. The Ronald Press, New York, NY. 546 pp.

Harrington, F.H. 1975. Response parameters of elicited wolf howling. Ph.D. Thesis, State Univ. of New York, Stony Brook, NY. 412 pp.

Harrington, F.H.; Paquet, P.C.; Ryon, C.J.; Fentress, J.C. 1982. Monogamy in wolves: a review of the evidence. Pages 209–222 *in* Harrington, F.H.; Paquet, P.C., eds. Wolves of the world: perspectives on behavior, ecology, and conservation. Noyes Publications, Park Ridge, NJ. 474 pp.

Harrison, D.L. 1968. The mammals of Arabia. 3 vols. Ernest Benn, Ltd., London, England. 670 pp.

Hauge, T.M.; Keith, L.B. 1981. Dynamics of moose populations in northeastern Alberta. J. Wildl. Manage. 45:573–597.

Hemmer, H. 1974. Untersuchungen zur stammesgeschichte der Pantherkatzen (Pantherinae). III. Zur Artgeschichte des Löwen *Panthera (Panthera) leo* (Linnaeus 1958). Veröff. Zool. Staatssaml. München 17:167–280.

Henshaw, J. 1968. The activities of wintering caribou in northwestern Alaska in relation to weather and snow conditions. Int. J. Biometeorol. 12:21–27.

Henshaw, J. 1970. Consequences of travel in the rutting of reindeer and caribou (*Rangifer tarandus*). Anim. Behav. 18: 256–258.

Hill, E.L. 1979. The ecology of the timber wolf (*Canis lupus* Linn.) in southern Manitoba — wilderness, recreational and agricultural aspects. Unpubl. M.Sc. Thesis, Univ. of Manitoba, Winnipeg, Man. 147 pp.

Horn, H.S. 1978. Optimal tactics of reproduction and life-history. Pages 411–429 *in* Krebs, J.R.; Davies, N.B., eds. Behavioural ecology: an evolutionary approach. Sinauer Assoc., Sunderland, MA. 494 pp.

Iljin, N.A. 1941. Wolf–dog genetics. J. Genet. 42:359–414.

Imaizumi, Y. 1970*a*. Systematic status of the extinct Japanese wolf, *Canis hodophilax*. J. Mammal. Soc. Jap. 5:27–32.

Imaizumi, Y. 1970*b*. Systematic status of the extinct Japanese wolf, *Canis hodophilax*. J. Mammal. Soc. Jap. 5:62–66.

Jolicoeur, P. 1959. Multivariate geographical variation in the wolf *Canis lupus* L. Evolution 13:283–299.

Jolicoeur, P. 1975. Sexual dimorphism and geographical distance as factors of skull variation in the wolf *Canis lupus* L. Pages 54–61 *in* Fox, M.W., ed. The wild canids. Van Nostrand Reinhold, New York, NY.

Jordan, P.A.; Shelton, P.C.; Allen, D.L. 1967. Numbers, turnover and social structure of the Isle Royale wolf population. Am. Zool. 7:223–252.

Joslin, P.W.B. 1967. Movements and homesites of timber wolves in Algonquin Park. Am. Zool. 7:279–288.

Keith, L.B. 1974. Some features of population dynamics in mammals. Proc. Congr. Game Biol. 11:17–58.

Kelker, G.H. 1947. Computing the rate of increase for deer. J. Wildl. Manage. 11:177–183.

Kelsall, J.P. 1968. The migratory barren-ground caribou of Canada. Can. Wildl. Serv. Monogr. No. 3, Ottawa. 340 pp.

Kleiman, D.G. 1980. The sociobiology of captive propagation. Pages 243–261 *in* Soule, M.E.; Wilcox, B.A., eds. Conservation biology: an evolutionary–ecological perspective. Sinauer Assoc., Sunderland, MA. 395 pp.

Kolenosky, G.B. 1971. Hybridization between wolf and coyote. J. Mammal. 52:446–449.

Kolenosky, G.B. 1972. Wolf predation on wintering deer in east-central Ontario. J. Wildl. Manage. 36:357–369.

Kolenosky, G.B.; Standfield, R.O. 1975. Morphological and ecological variation among gray wolves (*Canis lupus*) of Ontario, Canada. Pages 62–72 *in* Fox, M.W., ed. The wild canids. Van Nostrand Reinhold, New York, NY.

Krebs, C.J. 1972. Ecology: the experimental analysis of distribution and abundance. Harper and Row, New York, NY. 694 pp.

Krefting, L.W. 1951. What is the future of the Isle Royale moose herd? Trans. N. Am. Wildl. Conf. 16:461–470.

Krefting, L.W. 1974. The ecology of the Isle Royale moose with special reference to the habitat. Univ. of Minnesota Agric. Exp. Stn., Tech. Bull. 297, For. Ser. 15.

Krefting, L.W.; Erickson, A.B. 1956. Results of special deer hunts on the Mud Lake National Wildlife Refuge, Minnesota. J. Wildl. Manage. 20:297–302.

Kuyt, E. 1972. Food habits and ecology of wolves on barren-ground caribou range in the Northwest Territories. Can. Wildl. Serv. Rep. No. 21. Ottawa. 36 pp.

Lack, D. 1954. The natural regulation of animal numbers. Oxford Univ. Press, Oxford, England. 343 pp.

LaRoi, G.H.; Hampson, C.G.; Fuller, W.A.; Nyland, E. 1967. The boreal forest. Pages 151–191 *in* Hardy, W.S., ed. Alberta — a natural history. Hurtig Publ., Edmonton, Alta. 343 pp.

Lentfer, J.W.; Sanders, D.K. 1973. Notes on the captive wolf (*Canis lupus*) colony, Barrow, Alaska. Can. J. Zool. 51:623–627.

Leopold, A.S. 1964. Predator and rodent control in the United States. Pages 27–49 *in* Trefethen, J.B., ed. Transactions of the 29th North Am. Wildl. and Nat. Resour. Conf., Wildl. Manage. Inst., Washington, DC.

Leopold, A.S.; Darling, F.F. 1953. Wildlife in Alaska, an ecological reconnaissance. The Ronald Press Co., New York, NY. 129 pp.

LeResche, R.E.; Bishop, R.H.; Coady, J.W. 1974. Distribution and habitats of moose in Alaska. Naturaliste can. 101:143–178.

Lerner, I.M. 1954. Generic homeostasis. Oliver and Boyd, Edinburgh, Scotland. Dover ed. 134 pp.

Leveque, J.C. 1954. Arctic airborne wolf hunt. Alaska Sportsman 10:6–9, 38–40.

Lockwood, R.A. 1979. Dominance in wolves: useful construct or bad habit? Pages 225–244 *in* Klinghammer, E., ed. The behavior and ecology of wolves. Garland Press, New York, NY. 876 pp.

Lord, L.A. 1961. Un envahisseur importun. Carnets de zoologie 21:6–7.

Martin, F.R.; Krefting, L.W. 1953. The Necedah Refuge deer irruption. J. Wildl. Manage. 17:166–176.

Matthey, R. 1973. The chromosome formulae of eutherian mammals. Pages 531–616 *in* Chiarelli, A.B.; Capanna, E., eds. Cytotaxonomy and vertebrate evolution. Academic Press, New York, NY. 783 pp.

May, R.M. 1976. Models for single populations. Pages 4–25 *in* May, R.M., ed. Theoretical ecology. Blackwell Scientific Publications, Oxford, England. 317 pp.

Maynard Smith, J. 1978. The evolution of sex. Cambridge Univ. Press, Cambridge, England. 222 pp.

McCabe, R.A.; Kozicky, E.L. 1972. A position on predator management. J. Wildl. Manage. 36(2): 382–394.

McCowan, D. 1950. Animals of the Canadian Rockies. MacMillan Can., Toronto, Ont. 300 pp.

McDougall, J. 1898. Path finding on plain and prairie: stirring scenes of life in the Canadian northwest. William Brigg, Toronto, Ont. 277 pp.

Mech, L.D. 1966. The wolves of Isle Royale. Fauna of the National Parks of the US. Fauna Series No. 7. US Gov. Printing Office, Washington, DC. 210 pp.

Mech, L.D. 1970. The wolf: ecology and behavior of an endangered species. Natural History Press, Doubleday, New York, NY. 384 pp.

Mech, L.D. 1973. Wolf numbers in the Superior National Forest of Minnesota. US Dep. Agric. For. Serv. Res. Pap. NC-97, St. Paul, MN. 10 pp.

Mech, L.D. 1977*a*. Productivity, mortality, and population trends of wolves in northeastern Minnesota. J. Mammal. 58(4):559–574.

Mech, L.D. 1977*b*. Population trend and winter deer consumption in a Minnesota wolf pack. Pages 55–83 *in* Philipps, R.; Jonkel, C., eds. Proc. 1975 Predator Symposium. Bull. Montana For. Conserv. Exp. Stn., Univ. of Montana, Missoula, MT. 268 pp.

Mech, L.D.; Frenzel, Jr., L.D. 1971. Ecological studies of the timber wolf in northeastern Minnesota. US Dep. Agric. For. Serv. Res. Pap. NC-52, St. Paul, MN. 62 pp.

Mech, L.D.; Karns, P.D. 1977. Role of the wolf in a deer decline on the Superior National Forest. US Dep. Agric. For. Serv. Res. Pap. NC-148, St. Paul, MN. 23 pp.

Medjo, D.; Mech, L.D. 1976. Reproductive activity in nine- and ten-month old wolves. J. Mammal. 57:406–408.

Mercer, W.E.; Manuel, F. 1974. Some aspects of moose management in Newfoundland. Int. Symp. on moose ecology. Nat. Can. Presse de l'université Laval, Qué. 101:657–671.

Merriam, H.R. 1964. The wolves of Coronation Island. Page 27 *in* Dahlgren, G., ed. Proc. 15th Alaskan Sci. Conf. Alaska Div. of Am. Assoc. Adv. Sci., College, AK.

Millar, W.N. 1915. The big game of the Canadian Rockies. Conserv. of fish, birds, and game. Proc. of Comm. Meet., 1–2 Nov. 1915. The Methodist Book and Publ. House, Toronto, Ont. pp. 100–124.

Miller, F.L.; Broughton, E. 1974. Calf mortality during 1970 on the calving ground of the Kaminuriak caribou. Can. Wildl. Serv. Rep. Ser. No. 26. 26 pp.

Miller, F.L.; Broughton, E.; Gunn, A. (In press). Mortality of newborn migratory barren-ground caribou calves, Northwest Territories, Canada. Proc. 3rd Int. Reindeer/Caribou Symp., Saariselka, Finland, 23–26 August 1982.

Morton, W.L. 1957. Manitoba: a history. Univ. of Toronto Press, London, Ont. 519 pp.

Mowat, F. 1963. Never cry wolf. Little, Brown Co., Boston, MA. 247 pp.

Murie, A. 1944. The wolves of Mount McKinley. Fauna of the National Parks of the US. Fauna Series No. 5. US Gov. Printing Office, Washington DC. 238 pp.

Murie, O.J. 1954. A field guide to animal tracks. Houghton Mifflin Co., Boston, MA. 375 pp.

Mytton, W.R.; Keith, L.B. 1981. Dynamics of moose populations near Rochester, Alberta, 1975–1978. Can. Field-Nat. 95:39–49.

Nellis, C.H. 1968. Some methods for capturing coyotes. J. Wildl. Manage. 30:402–405.

Novikov, G.A. 1956. Carnivorous mammals of the fauna of the USSR. Israel Program for Scientific Translations, Jerusalem, Israel. (transl. 1962).

Nowak, R.M. 1973. North American Quaternary *Canis*. Ph.D. Thesis, Dep. of Systematics and Ecol., Univ. of Kansas, Lawrence, KS. 380 pp.

Nowak, R.M. 1975. The cosmopolitan wolf. Natl. Rifle Assoc. Conserv. Yearbook. pp. 76–82.

Nowak, R.M. 1978. Evolution and taxonomy of coyotes and related *Canis*. Pages 3–16 *in* Coyotes biology, behavior, and management. Academic Press, New York, NY. 383 pp.

Nowak, R.M. 1979. North American Quaternary *Canis*. Monogr. No. 6. Mus. Nat. Hist., Univ. of Kansas, Lawrence, KS. 154 pp.

O'Gara, B.W. 1978. Differential characteristics of predator kills. Proc. 8th Biennial Pronghorn Antelope Workshop. Jasper, Alta. pp. 380–393.

Oldemeyer, J.L.; Franzmann, A.W.; Brundage, A.L.; Arneson, P.D.; Flynn, A. 1977. Browse quality and the Kenai moose population. J. Wildl. Manage. 4(3):533–542.

Olson, S.T. Jr. 1979. The life and times of the black-tailed deer in southeast Alaska. Pages 160–168 *in* Wallmo, D.C.; Schoer, J.W., eds. Sitka black-tailed deer. Proc. Conf. in Juneau, AK. US Dep. Agric., For. Serv., Alaska Reg., and Alaska Dep. Fish & Game. Series No. R10 – 48.

Omand, D.N. 1950. The bounty system in Ontario. J. Wildl. Manage. 14:425–434.

Oosenbrug, S.M.; Carbyn, L.N. 1982. Winter predation on bison and activity patterns of a pack of wolves in Wood Buffalo National Park. Pages 43–53 *in* Wolves of the world: perspectives of behavior, ecology, and conservation. Noyes Publications, Park Ridge, NJ. 474 pp.

Packard, J.M. 1980. Deferred reproduction in wolves (*Canis lupus*). Ph.D. Thesis. Univ. of Minnesota, Minneapolis, MN. 335 pp.

Packard, J.P.; Mech, L.D. 1980. Population regulation in wolves. Pages 135–150 *in* Cohen, M.N.; Malpass, R.S.; Klein, H.G., eds. Biosocial mechanisms of population regulation. Yale Univ. Press, New Haven, CT. 406 pp.

Paquet, P.C.; Bragdon, S.; McCusker, S. 1982. Cooperative rearing of simultaneous litters in captive wolves. Pages 223–237 *in* Harrington, F.H.; Paquet, P.C., eds. Wolves of the world: perspectives on behavior, ecology, and conservation. Noyes Publications, Park Ridge, NJ. 474 pp.

Parker, G.R. 1971. Trends in the population of barren-ground caribou of mainland Canada over the last two decades: a re-evaluation of the evidence. Can. Wildl. Serv. Occ. Pap. No. 10, Ottawa. 11 pp.

Parker, G.R. 1972. Biology of the Kaminuriak population of barren-ground caribou. Part I: Total numbers, mortality, recruitment, and seasonal distribution. Can. Wildl. Serv. Rep. Ser. No. 20, Ottawa. 93 pp.

Parker, G.R. 1973. Distribution and densities of wolves within barren-ground caribou ranges in northern mainland Canada. J. Mammal. 57:341–348.

Parker, G.R. 1975. An investigation of caribou range on Southampton Island, Northwest Territories. Can. Wildl. Serv. Rep. Ser. No. 33, Ottawa. 83 pp.

Pederson, S. 1982. Geographical variation in Alaskan wolves. Pages 345–361 *in* Harrington, F.H.; Paquet, P.C., eds. Wolves of the world: perspectives on behavior, ecology, and conservation. Noyes Publications, Park Ridge, NJ. 474 pp.

Peterson, R.L. 1966. The mammals of eastern Canada. Oxford Univ. Press, Toronto. 465 pp.

Peterson, R.O. 1977. Wolf ecology and prey relationships on Isle Royale. US Natl. Park Serv. Fauna Ser. 11, Washington, DC. 210 pp.

Peterson, R.O.; Woolington, J.D. 1982. The apparent extirpation and reappearance of wolves on the Kenai Peninsula, Alaska. Pages 334–344 *in* Harrington, F.; Paquet, P., eds. Wolves of the world: perspectives of behavior, ecology, and conservation. Noyes Publications, Park Ridge, NJ. 474 pp.

Pimlott, D.H. 1959. Moose harvests in Newfoundland and Fennoscandian countries. Trans. N. Am. Wildl. Conf. 24:422–448.

Pimlott, D.H. 1961. Wolf control in Canada. Can. Aud. 23:145–152.

Pimlott, D.H. 1967*a*. Wolves and men in North America. Study No. 5. Defenders of Wildl. News. pp. 36–47.

Pimlott, D.H. 1967*b*. Wolf predation and ungulate populations. Am. Zool. 7:267–278.

Pimlott, D.H. 1970. Predation and productivity of game population in North America. Trans. Int. Congr. Game Biol. 9:63–72.

Pimlott, D.H.; Shannon, J.A.; Kolenosky, G.B. 1969. The ecology of the timber wolf in Algonquin Provincial Park, Ont. Dep. Lands and For. Res. Rep. Wildl. 87. Ottawa. 92 pp.

Pocock, R.I. 1935. The races of *Canis lupus*. Proc. Zool. Soc. London, 1935. Pt. 3. pp. 617–686.

Presnall, C.C. 1950. The predation question — facts versus fancies. Pages 197–208 *in* Quee, E.N., ed. Trans. 15th N. Am. Wildl. Conf., Wildl. Manage. Inst., Washington, DC.

Pulliainen, E. 1982. Experiences in the protection of the large predators in Finland. Int. J. Study Anim. Probl. 3(1):33–41.

Rabb, G.B.; Woolpy, J.H.; Ginsburg, B.E. 1967. Social relations in a group of captive wolves. Am. Zool. 7:305–311.

Ralls, K.; Brugger, K.; Ballou, J. 1979. Inbreeding and juvenile mortality in small populations of ungulates. Science 206:1101–1103.

Rausch, R.L. 1953. On the status of some arctic mammals. Arctic 6:91–148.

Rausch, R.A. 1961. Present status and possible future management of wolf populations in interior and arctic Alaska. Page 28 *in* Dahlgren, G., ed. Proc. 12th Alaskan Sci. Conf. Alaska Div., Am. Assoc. Adv. Sci., College, AK.

Rausch, R.A. 1964. Progress in management of the Alaskan wolf population. Page 43 *in* Dahlgren, G., ed. Proc. 15th Alaskan Sci. Conf. Alaska Div., Am. Assoc. Adv. Sci., College, AK.

Rausch, R.A. 1967. Some aspects of the population ecology of wolves, Alaska. Am. Zool. 7:253–265.

Rausch, R.A. 1969. A summary of wolf studies in southcentral Alaska, 1957–1968. Trans. Am. Wildl. and Nat. Resour. Conf. 34:117–131.

Rausch, R.A.; Hinman, R.A. 1975. Wolf management in Alaska — an exercise in futility? Pages 147–156 *in* Philipps, R.L.; Jonkel, C., eds. Proc. 1975 Predator Symp. Montana For. and Conserv. Exp. Stn., Univ. of Montana, Missoula, MT. 268 pp.

Ream, R.; Mattson, U. 1982. Wolf status in the northern Rockies. Pages 362–381 *in* Harrington, F.; Paquet, P., eds. Wolves of the world: perspectives of behavior, ecology, and conservation. Noyes Publications, Park Ridge, NJ. 474 pp.

Rearden, J. 1980. Wolf management in Alaska. Alaska 46(5):30.

Rich, E.E. 1967. The fur trade and the northwest to 1857. McClelland and Stewart Ltd., Toronto, Ontario. 336 pp.

Riewe, R. 1975. The high arctic wolf in the Jones Sound Region. Arctic 28:209–212.

Rich, E.E. 1949. Isham's observations and notes (1743–49). Champlain Society, Toronto. 352 pp.

Rodney, W. 1969. Kootenai Brown: his life and times, 1839–1916. Gray's Publ. Ltd., Sidney, B.C. 251 pp.

Rowan, W. 1950. Winter habits and numbers of timber wolves. J. Mammal. 31:167–169.

Rowe, J.S. 1972. Forest regions of Canada. Can. For. Serv. Publ. 1300. Ottawa, Ont. 172 pp.

Roy, L.D.; Dorrance, M.J. 1976. Methods of investigating predation of domestic livestock: a manual for investigating officers. Alta. Agric. Rep. 54 pp.

Rutter, R.J.; Pimlott, D.H. 1968. The world of the wolf. J.P. Lippincott, Philadelphia, PA. 202 pp.

Samuel, W.M.; Chalmers, G.A.; Gunson, J.R. 1978. Oral papillomatosis in coyotes (*Canis latrans*) and wolves (*Canis lupus*) of Alberta. J. Wildl. Dis. 14:165–169.

Schenkel, R. 1967. Submission: its features and functions in the wolf and dog. Am. Zool. 7:319–330.

Scott, B.M.V. 1979. The Vancouver Island wolf (*Canis lupus crassodon*), an initial study of food habits and social organization. M.Sc. Thesis, Dep. Anim. Sci., Univ. of British Columbia, Vancouver, B.C. 112 pp.

Scott, B.M.V.; Shackleton, D.M. 1980. Food habits of two Vancouver Island wolf packs: a preliminary study. Can. J. Zool. 58:1203–1207.

Seal, U.S.; Plotka, E.O.; Packard, J.M.; Mech, L.D. 1979. Endocrine correlates of reproduction in the wolf: I. Serum progesterone, estradiol and LH during the estrous cycle. Biol. Reprod. 21:1057–1066.

Senner, J.W. 1980. Inbreeding depression and the survival of zoo populations. Pages 209–224 *in* Soule, M.E.; Wilcox, B.A., eds. Conservation biology. Sinauer Assoc., Sunderland, MA. 395 pp.

Seton, E.T. 1929. Lives of game animals. Vol. 1. Doubleday, Doran & Co. Inc., Garden City, NY. 640 pp.

Shields, W.M. 1982. Philopatry, inbreeding, and the evolution of sex. State Univ. of New York Press, Albany, NY. 245 pp.

Simmons, N.M.; Heard, D.C.; Calef, G.W. 1979. Kaminuriak caribou herd: Inter-jurisdictional management problems. Trans. N. Am. Wildl. and Nat. Resour. Conf. 44:102–126.

Skeel, M.A.; Carbyn, L.N. 1977. The morphological relationship of gray wolves (*Canis lupus*) in national parks of central Canada. Can. J. Zool. 55:737–747.

Skoog, R.O. 1968. Ecology of the caribou (*Rangifer tarandus granti*) in Alaska. Ph.D. Thesis, Univ. of California, Berkeley, CA. 699 pp.

Smith, P.C.; Borczon, E.L. 1977. Managing for deer and timber. Your Forests 10:1–12.

Smith, R.H. 1979. On selection for inbreeding in polygynous animals. Heredity 43:205–211.

Soper, J.D. 1928. A faunal investigation of southern Baffin Island. Natl. Mus. of Can., Ottawa. Bull. No. 53, Biol. Ser. No. 15. 143 pp.

Soper, J.D. 1948. Mammal notes from the Grande Prairie — Peace River region, Alberta. J. Mammal. 29:49–64.

Soper, J.D. 1964. The mammals of Alberta. Hamly Press, Edmonton, Alta. 402 pp.

Soule, M.E. 1980. Thresholds for survival: maintaining fitness and evolutionary potential. Pages 151–169 *in* Soule, M.E.; Wilcox, B.A., eds. Conservation biology. Sinauer Assoc., Sunderland, MA. 395 pp.

Soule, M.E.; Wilcox, B.A., eds. 1980. Conservation biology. Sinauer Assoc., Sunderland, MA. 395 pp.

Spencer, D.L.; Hakala, J.B. 1964. Moose and fire on the Kenai. Tall Timbers Fire Ecol. Conf. 3:11–33.

Spry, I.M. 1963. The Palliser expedition. MacMillan Can., Toronto, Ont. 310 pp.

Standfield, R.O. 1970. A history of timber wolf (*Canis lupus*) populations in Ontario, Canada. Trans. 9th Int. Congr. of Game Biol., Moscow, USSR. pp. 505–513.

Stelfox, J.G. 1969. Wolves in Alberta: a history 1800–1969. Alta. Lands, Forests, Parks, Wildlife 12:18–27.

Stenlund, M.H. 1955. A field study of the timber wolf (*Canis lupus*) on the Superior National Forest, Minnesota. Minnesota Dep. Conserv. Tech. Bull. 4. 55 pp.

Studley, J.T. 1912. The journal of a sporting nomad. John Lane Co., New York, NY. 303 pp.

Theberge, J.B. 1973. Wolf management in Canada through a decade of change. Nat. Can. 2:3–10.

Theberge, J.B. 1977. Wolves: Canadian perspective. Pages 51–54 *in* Mosquin, T.; Suchal, C., eds. Canada's threatened species and habitats. Can. Nat. Fed., Ottawa, Ont. 185 pp.

Theberge, J.B.; Falls, J.B. 1967. Howling as a means of communication in timber wolves. Am. Zool. 7:331–338.

Theberge, J.B.; Strickland, D.R. 1978. Changes in wolf numbers, Algonquin Provincial Park, Ontario. Can. Field-Nat. 92:395–398.

Thomas, D.C. 1981. At the crossroads of caribou management in northern Canada. Can. Nat. Fed., Ottawa, Ont. Spec. Publ. No. 10. 21 pp.

Thompson, D.C.; Fischer, C.A. 1979. Distribution and numbers of the Kaminuriak caribou herd in March and April, 1977. Arctic 32:266–274.

Todd, A.W.; Geisbrecht, L.C. 1979. A review of Alberta fur production and management, 1920–21 to 1977–78. Alta. Fish and Wildl. Div. Rep., Edmonton. 28 pp.

Todd, A.W.; Gunson, J.R.; Samuel, W.M. 1981. Sarcoptic mange, an important disease of coyotes and wolves of Alberta. *In* Chapman, J.A.; Pursley, D., eds. Proc. 1st Worldwide Furbearer Conf., 3–11 Aug. 1980, Frostburg, MD.

Tolstoy, Leo. 1862. The Cossacks. Penguin translation by Rosemary Edmonds, 1960.

Tompa, F.S. 1980. Vertebrate pest management in British Columbia. Pages 76–81 *in* Proc. 27th Annu. Meet. Can. Pest. Manage. Soc., Edmonton, Alta.

United States Fish and Wildlife Service. 1967. Div. of Wildl. Serv., Policy Handbook. Washington, DC.

United States Fish and Wildlife Service. 1979. Mammalian predator damage management for livestock protection in the western United States. Final Environ. Impact Statement. Dep. Int., Washington, DC. 787 pp.

Usher, P.J. 1971. The Banks islanders: economy and ecology of a frontier trapping community. Vol. 2. Economy and ecology. Northern Sci. Res. Group. Dep. Indian Affairs and Northern Development. NSRG 71-4. 180 pp.

Van Ballenberghe, V. 1981. Population dynamics of wolves in the Nelchina Basin, southcentral Alaska. Pages 1246–1258 *in* Chapman, J.A.; Pursley, D.P., eds. Proc. Worldwide Furbearer Conf., Frostburg, MD.

Van Ballenberghe, V.; Erickson, A.W.; Byman, D. 1975. Ecology of the timber wolf in northeastern Minnesota. Wildl. Monogr. 43:1–43.

Van Camp, J.; Gluckie, R. 1979. A record long-distance move by a wolf (*Canis lupus*). J. Mammal. 60:236–237.

Van Etten, R.C.; Switzenberg, D.F.; Eberhardt, L. 1965. Controlled deer hunting in a square mile enclosure. J. Wildl. Manage. 29:59–73.

Van Noordwijk, A.J.; Scharloo, W. 1981. Inbreeding in an island population of the Great Tit. Evol. 35:674–688.

Van Valen, L. 1965. Morphological variation and the width of the ecological niche. Am. Nat. 94:377–390.

Vincent, D.; Gunn, A. 1981. Population increase of muskoxen on Banks Island and implications for competition with Peary caribou. Arctic 34:175–179.

Voigt, D.R. 1973. Summer food habits and movements of wolves (*Canis lupus*) in central Ontario. Ms. Thesis, Univ. of Guelph, Guelph, Ont. 76 pp.

Voigt, D.R.; Kolenosky, G.B.; Pimlott, D.H. 1976. Changes in summer foods of wolves in central Ontario. J. Wildl. Manage. 40:663–668.

Weaver, E.P. 1913. The Counties of Ontario. Bell and Cockburn, Toronto, Ont. 318 pp.

Weaver, J.L.; Fritts, S.H. 1979. Comparison of coyote and wolf scat diameters. J. Wildl. Manage. 43:786–788.

Weener, R. 1976. Alaska Conservation Society and western arctic caribou–wolf problem. Alaska Conserv. Rev. 17:6–7.

White, M.J.D. 1973. Descriptions of remains of deer fawns killed by coyotes. J. Mammal. 54:291–293.

White, M.J.D. 1978. Modes of speciation. W.H. Freeman, San Francisco, CA. 455 pp.

Wickler, W. 1972. The sexual code. Doubleday Press, Garden City, NJ. 301 pp.

Wiley, R.H. 1974*a*. Evolution of social organization and life-history patterns among grouse. Quart. Rev. Biol. 49:201–227.

Wiley, R.H. 1974*b*. Effects of delayed reproduction on survival, fecundity, and the rate of population increase. Am. Nat. 108:705–709.

Williams, G.C. 1975. Sex and evolution. Princeton Univ. Press, Princeton, NJ. 200 pp.

Williams, M.Y. 1946. Notes on the vertebrates of the southern plains of Canada; 1923–1926. Can. Field-Nat. 60:47–60.

Wilson, A.C.; Bush, G.L.; Case, S.M.; King, M.C. 1975. Social structuring of mammalian populations and rate of chromosomal evolution. Proc. Natl. Acad. Sci. 72(12):5061–5065.

Wilson, E.O.; Bossert, W.H. 1971. A primer of population biology. Sinauer Assoc., Stamford, CT.

Wittenberger, J.R. 1979. A model for delayed reproduction in iteroparous animals. Am. Nat. 114:439–446.

Wolfe, M.L.; Allen, D.L. 1973. Continued studies of the status, socialization and relationships of Isle Royale wolves 1967–1970. J. Mammal. 54:611–635.

Woolpy, J.H. 1968. The social organization of wolves. Nat. Hist. 77:46–55.

Wright, S. 1931. Evolution in mendelian populations. Genetics 16:97–159.

Wright, S. 1969. Evolution and the genetics of populations. Vol. 2. Theory of gene frequencies. Univ. of Chicago Press, Chicago, IL. 470 pp.

Wright, S. 1977. Evolution and the genetics of populations. Vol. 3. Experimental results and evolutionary deductions. Univ. of Chicago Press, Chicago, IL. 614 pp.

Wright, S. 1978. Evolution and the genetics of populations. Vol. 4. Variability within and among populations. Univ. of Chicago Press, Chicago, IL. 580 pp.

Young, S.P. 1944. The wolves of North America. Part I: Their history, life habits, economic status, and control. Am. Wildl. Inst., Washington, DC. Dover Publ., New York, NY. 385 pp.

Young, S.P.; Goldman, E.A. 1944. The wolves of North America. Am. Wildl. Inst., Washington, DC. Dover Publ., New York, NY.

Zimen, E. 1975. Social dynamics of the wolf pack. Pages 336–362 *in* Fox, M.W., ed. The wild canids: their systematics, behavioral ecology, and evolution. Van Nostrand Reinhold Co., New York, NY.

Zimen, E. 1976. On the regulation of pack size in wolves. Zeit. für Tierpsych. 40:300–341.

Zimen, E. 1982. A wolf pack sociogram. Pages 282–322 *in* Harrington, F.H.; Paquet, P.C. eds. Wolves of the world: perspectives on behavior, ecology, and conservation. Noyes Publications, Park Ridge, NJ. 474 pp.

Zimen, E.; Boitani, L. 1979. Status of the wolf in Europe and the possibilities of conservation and reintroduction. Pages 43–83 *in* Klinghammer, E., ed. Proceedings of the behavior and ecology of wolves. Garland STPM Press, New York, NY.

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