The Wildlife Society

Management of Large Mammalian Carnivores in North America

Technical Review 12-01
August 2012

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Large center photo: Radio-collared gray wolf (Credit: William Campbell/U.S. Fish and Wildlife Service)

Top right: Collecting data from tranquilized grizzly bear in Glacier National Park prior to attaching a radio collar (Credit: National Park Service)

Bottom left: U.S. Fish and Wildlife Service biologists collecting data and fitting a radio collar on a tranquilized mountain lion in Charles M. Russell National Wildlife Refuge in Montana (Credit: U.S. Fish and Wildlife Service)

Bottom right: Coyote roaming Waterfall Glen Forest Preserve (Credit: Photo by George Joch/Courtesy Argonne National Laboratory, Lemont, Illinois)

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FOREWORD

Presidents of The Wildlife Society (TWS) occasionally appoint *ad hoc* committees to study and report on selected conservation issues. The reports ordinarily appear as technical reviews or position statements. Technical reviews present technical information and the views of the appointed committee members, but not necessarily the views of their employers.

This technical review focuses on the management of large mammalian carnivores and their associated impacts on prey populations and public perception across North America. The review is copyrighted by TWS, but individuals are granted permission to make single copies for noncommercial purposes. All technical reviews are available in digital format on the TWS web page, **www.wildlife.org**, and additional copies may be requested from:

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A large share of the information in this report is available from wildlife agencies across Canada and the United States. Much of the information is routinely obtained to assist in managing large carnivores and their ungulate prey. An additional share of the information is supported by various wildlife agencies and developed by others. We received exceptional cooperation from people in these agencies when we requested information.

Humans are primarily focused on the contemporary local situation they find themselves in. The wildlife resource, however, is affected by past and present conditions and multi-scale influences. As a result, many of the actions intended to address an issue that is considered in unsatisfactory condition may be successful in the short term but may also have unintended future consequences. Our efforts were, thus, directed towards detecting large-scale trends over time in more reliable data sources, primarily harvest information, and in surveys of public attitudes towards large mammalian carnivores.

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INTRODUCTION

The practice of managing larger mammalian carnivores is an example of how principles, information, and pragmatism conflict. Human attitudes towards large carnivores are typically inversely proportional to their abundance. People value carnivores more when they become rare (Schwartz et al. 2003), which is reflected in contemporary beliefs and perceptions. Large carnivores that prey on ungulates and threaten public safety and livelihoods remain among the most difficult populations to conserve and manage. Carnivore population levels in today's multi-use landscapes depend on ecological carrying capacity (KCC) and on social carrying capacity—the tolerance of people towards these predators (Breitenmoser et al. 2005). Wildlife managers should consider public demands to protect wildlife from people and protect people and property from wildlife (Treves and Naughton-Treves 2005).

This review addresses the current management of larger mammalian carnivores to increase, maintain, or reduce their numbers, while taking into account the population of certain ungulate prey and their relation to predators, social pressures and attitudes of the public towards predators, and the effects of sport hunting and trapping on carnivore population dynamics. This review considers brown bears (*Ursus arctos*), black bears (*U. americanus*), coyotes (*Canis latrans*), wolves (*Canis lupus, C. lycaon*), and mountain lions (*Felis concolor*). The appendix presents the results of a statistical analysis of trends discussed in this report.

A Brief History

Larger carnivores invoke public interest in wildlife management and conservation. Public involvement with their management has become common, increasing attention on wildlife management agencies. Conflicts over predator management involve a concerned public and organizations that have opposing views.

Though public influences affect agency policy and decisions, the attention also yields benefits for wildlife resources. From a professional viewpoint, the most positive influence is the development of a more comprehensive information base on larger predators. Increased information is a major factor enabling managers to advance management and conservation of predators in the face of controversy. A scientific approach to management involving an adaptive component is a pragmatic and defensible policy. When controversy results in judicial involvement, scientifically defensible information is critical in that decision-making process.

Studies of large predators began increasing in the 1960s. Investigations of the grizzly (*Ursus arctos horribilis*) in Yellowstone National Park (Yellowstone) (Craighead and Craighead 1969), the African lion (*Panthera leo;* Schaller 1972), the wolf studies on Isle Royale (Allen 1979), and the mountain lion investigations in the central Idaho wilderness (Hornocker 1970) all captured broad public interest. Initially the effects of predators on prey were the major focus, but eventually it became important to understand the biology of the predators to properly manage them.

Earlier investigations minimized the influence of predators on prey. Errington (1946) concluded that most predation was superfluous in affecting prey populations, although recognition that predation by members of the dog family might be the exception is noted. Pearson's (1975) grizzly studies emphasized the importance of vegetation for this species in the southern Yukon. Over 52 years of study, wolves and moose (*Alces alces*) have coexisted on Isle Royale in a highly dynamic equilibrium related to winter severity and forage availability for moose (Vucetich and Peterson 2011). Hornocker (1970) reported increasing elk (*Cervus canadensis*) and stable mule deer (*Odocoileus hemionus*) populations in the face of mountain lion predation in central Idaho. Pimlott et al. (1969) reported that wolves were the major mortality factor for white-tailed deer (*Odocoileus virginianus*) in Algonquin Park, Ontario, but were unable to show that the predation was limiting. The finding of lynx (*Lynx canadensis*) being a major mortality factor for caribou (*Rangifer* *tarandus*) calves on a Newfoundland calving ground provided additional evidence of the role of predators, even as those caribou populations were reportedly increasing at that time (Bergerud 1971).

All of these studies were conducted in areas where human influences were minimized, including parks and wilderness areas. Howard (1974) recognized that once environments were modified by humans, management of their components inevitably followed. In retrospect, human dimensions were an important aspect of contemporary management issues involving predators, wherein their prey was exploited and habitats were modified, either inadvertently as through protection from fire, or purposefully as through logging, grazing, or development. There is a need to recognize that studies of ecosystems that are protected as much as possible from human intrusions may yield information that, while useful in furthering understanding, may not be applicable in areas where active management of one component or another is taking place. Further, elimination of human influences may not reflect natural conditions, since human beings have inhabited North America for centuries.

Cain et al. (1972) provided a comprehensive review of coyote management in the U.S. President Nixon signed an executive order prohibiting use of poisons that were found to cause extensive mortality of non-target species that scavenged on poison baits and carcasses. The now defunct Predator and Rodent Control Division within the U.S. Fish and Wildlife Service (FWS) was reformed to become Wildlife Services with improved standards of training for its employees. Predator control in wilderness areas was eliminated.

When the wolf was declared a threatened species in 1974 and the grizzly bear in 1975, the Endangered Species Act provided impetus to increase populations of these species. The grizzly bear population in Yellowstone, estimated at 136 at its lowest level, increased to levels approaching 650 by 2007 (Interagency Grizzly Bear Committee 2011) and was delisted in 2008 amidst heavy opposition from some groups, and relisted in 2009 after litigation. When wolves were translocated into central Idaho and Yellowstone, conflicts between competing interests became virtually inevitable. Investigations of grizzly and wolf ecology in Yellowstone provided an extensive information base that is still used to inform policy and management. These investigations, however, did not extend to the central Idaho region as information in this area was much more difficult to obtain (Smith et al. 2010).

Investigations of the effects of wolf predation on ungulates date back to Murie (1944) in Alaska, Cowan (1947) in western Canada, Mech (1966) on Isle Royale, Michigan, and Pimlott (1969) in Algonquin Park, Ontario. Wolves then preferred to prey on young-of-the-year, older, and infirm animals, although the preference may have been more apparent when prey were at high densities (Potvin et al. 1988). Investigations across the range of translocated wolves in central Idaho and the Yellowstone region confirmed this (Husseman et al. 2003, Smith et al. 2003). More recently, wolf populations have been implicated in reducing ungulate prey, strongly suggesting inversely density-dependent (depensatory) predation (White et al. 2010). The combined effects of human harvests and predation were implicated, which are often difficult to distinguish.

The investigations by Gasaway et al. (1983) of the effects of wolf predation on caribou and moose on the Tanana Flats south of Fairbanks, Alaska, provided an early and comprehensive look at the consequences of increased wolf populations. Their studies involved documenting the effects of predation prior to and after removal of wolves over a 4-year period. Results included estimates of moose survival to breeding age. The research showed that predation was suppressing moose populations to levels considered below the KCC.

Wolves contributed to declines of white-tailed deer in northeastern Minnesota during a period when habitat conditions were deteriorating and a series of severe winters were occurring (Mech and Karns 1977). Interactions between winter severities, forage conditions, and predation on big game thus began to be recognized as an important cause of population fluctuations.

Early on, black bears were identified as major predators of young-of-the-year (LeResche 1968, Schlegel 1976). As a result, as predators increased in range and numbers, management to increase or maintain harvest and populations of big game through reductions in predators became a source of conflict and controversy.

A review of Alaska's predator management history (Regelin 2002) reported the complexity and difficulty of managing large predators, with implications across the continent. Regelin (2002) concluded that it was highly unlikely the Alaska Department of Fish and Game (ADFG) would conduct widespread and continuous wolf control to increase ungulate populations because of high costs and public opposition. Localized wolf control by ADFG personnel could be used in select areas to help restore moose or caribou populations, but citizen participation in a planning process, wherein reliable scientific information guides decisions, would be necessary. Due to the extreme polarization of public opinion, statewide planning efforts were not successful and each area had to be addressed individually. Local residents and hunters would have to reduce predator populations through legal means of hunting bears and hunting or trapping wolves. Efforts by the agency to involve as many of the interested public as possible would be necessary.

Thus, management of large predators has been slowly changing from attempts to recover populations from low numbers in the early 20th century to managing population levels in the early 21st century. Exceptions include situations where populations have been designated endangered or threatened in the U.S., or sensitive in Canada, and efforts to restore viable populations are ongoing. Generally, as ungulate prey has increased, and human tolerance and support for retaining large predators has increased, harvest has been better regulated, and these species have benefitted. The task now is to manage populations at levels compatible with other needs and values to ensure that public understanding will continue to improve and tolerance will be maintained.

ATTITUDES TOWARDS PREDATORS

Reviews of attitudes towards wolves and coyotes are included in this section, with information on bears and mountain lions following in subsequent sections. Distinctions in attitudes toward predators occur among different sociodemographic groups. Generally, rural residents have more utilitarian, dominant, or negative attitudes towards wildlife while residents of metropolitan areas have more natural, ecological, or moral attitudes towards wildlife (Kellert and Berry 1980, Kertson 2005). Positive attitudes towards predators were correlated with pro-environmental beliefs while negative attitudes were connected to beliefs that humans were superior in relation to nature and wildlife (Kaltenborn et al. 1998). Kellert (1985) reported that individuals who viewed predators favorably were generally more concerned about animal welfare. Groups found to be most affectionate towards wildlife were members of wildlife and environmental protection agencies, bird watchers, backpackers, and those who hunt to be close to nature (Kellert 1985).

Educated urban youth were most supportive of carnivore conservation efforts though they were far removed from the animals themselves (Schwartz et al. 2003). In contrast, attitudes of farmers, livestock owners, and rural residents who had direct contact and experience with wolves and other predators were likely to hold the strongest negative attitudes because tolerance of these animals had direct negative economic consequences for them (Williams et al. 2002). A random survey among U.S. households reported that Americans were generally knowledgeable about predators and very supportive of their existence (Messemer et al. 1999).

Perceptions of individual species by the public originated from a diversity of factors including relationship of the animal to people, the size and intelligence of the species, its cultural relationship, aesthetic value, perceived danger of the animal, or threat to property (Kellert 1994). Kellert (1985) reported that predators as a group were generally disliked, in comparison to birds and domestic animals, although Americans appreciated mammalian species more than reptiles or fish. Animals were also favored if they were attractive or belonged to an evolutionarily advanced class (Kellert 1985). Predators were least liked by groups of low income or education, nonwhites, ranchers, residents of the South, and those of older ages. Further, Treves (2009) concluded that scientific measures of public support for carnivore-hunting policies were lacking.

Residents of Anchorage, Alaska, are generally tolerant of wildlife, and substantial populations of black bears, brown bears, and moose occur in the vicinity (Responsive Management 2010). Surveys reveal a relatively high level of knowledge of residents involving these species, which undoubtedly has a positive effect on tolerance levels. Most residents do not support killing bears just because they are seen in town, but do support destruction of specific bears by wildlife professionals when they threaten human safety. There is less support for killing bears that get into garbage, quite likely because there are simple steps people can take to minimize this potential conflict.

Attitudes towards Wolves and Wolf Reintroduction

Of 33 species included in a nationwide public survey (Kellert 1978), wolves and coyotes were among the least liked. Alaskans possessed the most positive perceptions of wolves, while sheep and cattle ranchers expressed very negative opinions (Kellert 1985). A comprehensive analysis of all wolf studies in North America and abroad (Williams et al. 2002) from 1972 to 2000 reported that 51% of all respondents held positive attitudes towards wildlife and that 60% supported restoration of wolf populations. The authors reported a negative correlation between attitudes and older respondents, ranchers, farmers, and rural residents, and positive correlations among respondents with higher income and education. A large majority (69%) of those respondents belonged to wildlife advocacy groups and held positive attitudes towards wolves, while only 35% of livestock ranchers surveyed viewed wolves in a positive manner. Seven out of 9 studies examined showed overwhelmingly negative attitudes of ranchers, as wolves represented a negative economic impact to this social group (Williams et al. 2002). This analysis revealed that people with the least experience with wolves had the most positive perceptions of this species, as the greatest support for wolf recovery came from urban residents and those respondents belonging to environmental organizations. Williams et al. (2002) concluded that attitudes towards wolves would likely become more positive in areas where people were isolated from nature and more negative in areas of wolf recovery.

Regional differences in attitudes towards wolves were apparent. A recent study suggested that Minnesota residents perceived wolves to be a much greater threat than all other carnivores (Chavez et al. 2005). In previous studies, landowners in Minnesota agreed that wolves continued to be a threat to livelihoods but listed other factors as greater threats to profitable agriculture (Fuller et al. 1992). Residents of Montana (58%) expressed positive attitudes towards wolves if their occurrence did not limit human activities like hunting (Tucker and Pletscher 1989). Native American groups in Wisconsin opposed wolf removal due to strong cultural and symbolic significance (Treves and Naughton-Treves 2005).

There was speculation among wildlife managers that resolutions to address conflicts through compensation for losses would alleviate negative attitudes. Compensation seemed like a preferable option to those living among carnivores because it moved the economic responsibility to a larger public domain. However, there was little quantitative evidence to support compensation programs as facilitators of increased tolerance and positive attitudes towards wildlife and conservation (Nyhus et al. 2005).

Treves and Karanth (2003) studied the impact of compensation on residents' attitudes towards predators and reported that a resident's social group was the strongest predictor of wolf tolerance. Rural residents in Wisconsin approved of compensation options to resolve human-predator conflict in their state, however livestock producers who had been compensated for losses in the past were not more tolerant that those who had not received compensation (Treves and Karanth 2003). More information on local attitudes before and after a compensation program has been initiated would be helpful for managers to further analyze this potential solution to human-wolf conflict.

Enck and Brown (2002) used the Wildlife Attitudes and Values Scale to identify differences between residents living close to a wolf reintroduction site and statewide respondents. Residents near New York's proposed Adirondack Park reintroduction site were equally supportive and opposed to the plan (41% and 42%, respectively) whereas statewide residents generally supported the project (60%). Respondent attitudes were related to general attitudes towards wildlife, knowledge of the wolf, beliefs about positive or negative impacts of the restoration project, and media coverage seen on the topic. Perceived positive impacts of wolf reintroduction to Adirondack Park included balancing the deer population (55%) and returning a missing component of wilderness (53%). Respondents' perceived importance of this issue had a moderating effect on their attitudes (Enck and Brown 2002). Attitudes of special interest groups towards gray wolf reintroduction in New Brunswick, Canada, were most negative among hunters in areas with closed seasons due to low populations of white-tailed deer (Lohr et al. 1996). Generally, no groups were very supportive of a reintroduction, and the differences among groups were not significant. As indicated in other studies, positive attitudes were associated with higher education. The most common reason for opposing wolf reintroductions was the likely impact on deer populations and a prominent reason for supporting recovery was that wolves were historically present in the area (Lohr et al. 1996). Sixty-three percent of Mexican citizens questioned about translocation and reintroduction of wolves in their country were supportive and 50% of those against wolf reintroduction claimed they would change their opinion if compensation for livestock losses was available (Rodriguez et al. 2003). As a group, Mexican cattle ranchers held the most negative opinions, though unlike studies of attitudes in Canada and the U.S., no connection between opinion and age, gender, or place of residence was observed.

The Yellowstone wolf reintroduction received over 100,000 comments from residents of over 40 countries with interest in contributing to the Environmental Impact Statement. Of those surveyed by social scientists, Wyoming respondents, ranchers, and farmers expressed the most negative opinions of the project (Bath and Buchanan 1989). A slight majority of Idaho respondents (53.3%) supported the Yellowstone reintroduction as did almost half of Montanan respondents (44.7%). Fifty-five percent of respondents claimed the issue of reintroduction in Yellowstone was important to them, and the most common reason given for supporting reintroduction was because wolves were historically present.

Surveys questioned respondents about wolf management in Yellowstone and a majority agreed that if a translocated wolf preyed upon livestock it should be killed. Some respondents (27% in Montana and 25% in Idaho) said they would change their negative opinion of wolves if the wolves could be contained within the park. Montanans supporting wolf recovery were among the more educated and tended to be younger than those opposed (Bath 1992).

Duffield (1992) concluded that the net social benefits of the wolf recovery were large and very positive, greatly outweighing the costs associated with livestock depredation. Despite the positive aspects of the Yellowstone wolf recovery, humans caused 85% of adult wolf mortality in the northern Rocky Mountains (Bangs et al. 1995), and illegal killing was likely the single greatest cause of adult wolf deaths (Bangs et al. 2005).

PHOTO CREDIT: Dennis L. Murray/Trent University

This gray wolf belongs to the experimental population reintroduced to Yellowstone National Park by the U.S. Fish and Wildlife Service starting in 1995. These wolves are the subject of extensive investigations by scientists to determine population size and composition, movements and food habits.

A review of attitude surveys towards wolves (Bruskotter et al. 2010) suggested that attitudes were becoming less favorable in the Idaho-Montana-Wyoming recovery zone. High proportions of hunters and livestock owners were supportive of keeping populations at minimum levels required to keep them off of the Endangered Species list. Their review concluded that localized opposition to wolves was unlikely to change, and was not susceptible to education campaigns. Hunting wolves may encourage hunters to support wolf conservation, but hunter support was not discernible in surveys conducted from 2001 to 2007 (Treves and Martin 2011).

Attitudes towards Coyotes

Very little information has been published on attitudes towards coyotes, beyond the early studies of Kellert (1985). A nationwide survey of agricultural producers regarding wildlife damage (Conover 2003) found that 24% of those surveyed reported damage caused by coyotes. Agricultural producers in the Great Plains region experienced problems with coyotes more often than other regions of the country (Conover 2003). Green et al. (1984) reported that coyote depredation on livestock was an important economic issue for many farmers.

Many Vancouver, British Columbia, residents indicated willingness to alter their lifestyle to benefit the well-being of wildlife, but 21% expressed negative attitudes towards coyotes (Webber 1997). An overwhelming number (98%) of Florida cattle ranchers perceived the number of coyotes in Florida to be increasing, and many (69%) believed coyotes were causing a decline in wildlife on their ranches (Main et al. 2003). A majority of ranchers expressed interest in knowing more about coyotes in Florida and suggested there was a need for scientific research on impacts in the state. Martinez-Espineira (2006) reported that lethal coyote control was acceptable to Prince Edward Island residents when the animals were causing damage. All polls showed that older respondents more often agreed with lethal control, as did dog owners, hunters, those who approve of hunting, and those who had recently seen a coyote.

A survey of interactions between people and coyotes in suburban New York indicated that a majority of Westchester County residents were aware of coyote presence in their towns, were accepting of them, and had even experienced an encounter (Wieczirek Hudenko et al. 2008). Those surveyed believed the majority of residents would be unaware of coyotes, uninformed about them, and would be less accepting of their presence due to perceived threats against children and pets. Due to these perceptions, most respondents did not believe coyotes would present an issue for their communities (Wieczirek Hudenko et al. 2008). Coyotes have been reported in downtown New York and Los Angeles. Carbyn (1989) described coyote attacks on children in the western Canadian national parks in the 1980s, attributing them to loss of fear of humans and indications that children were regarded as prey. Attacks on humans by coyotes in Cape Breton Highlands National Park resulted in one death (Mellor 2010). Another death attributable to coyotes occurred in California in 1981 (Timm and Baker 2007), illustrating the need to minimize contact and resultant conditioning of all large mammalian predators. Trapping is the most effective tool for removing problem coyotes in urban situations (Baker 2007). Trapping, calling, and shooting are important in retaining fear of humans in coyotes.

UNGULATE POPULATION DYNAMICS AND PREDATION

The variability of interactions between population size, productivity, and survival has profound effects on predation as theoretical considerations suggest. Macnab (1985) reported how pressures to manage mule deer populations by retaining high densities of adult females can actually work in reverse of keeping productivity and hunter harvest high. Extensive literature exists demonstrating how high density ungulate populations show lower production of young than lower density populations (Cheatum and Severinghaus 1950, Caughley 1971, 1976, McCullough 1979, Festa-Bianchet and Jorgenson 1988, Coulson et al. 1997, Singer et al. 1997, White and Bartmann 1998, Keyser et al. 2006, Stewart et al. 2005, 2006, Morellet et al. 2007). However, these investigations were accomplished with populations that were not associated with a substantial complement of predators, and all showed low predation on neonates.

Higher production at population densities that exist at levels below KCC is expected, but higher survival of young does not necessarily follow. Very high and additive neonatal mortality may occur when populations are at low levels, production is high, predators are abundant or severe winter conditions or prolonged summer drought occurs (Bergerud 1971, Gasaway et al. 1983, 1992, Boertje et al. 1987, Ballard et al. 1991, Osborne 1991, Caughley and Gunn 1993, Adams et al. 1995, Crete 1999, Keech et al. 1999, Keech 2005, Hayes et al. 2003, Mahoney and Weir 2008, White et al. 2010). Wang et al. (2009) concluded from a review of density dependence in ungulates that hypotheses predicting herbivore biomass to increase as net primary productivity increases—but to remain constant in the presence of predators—applies to systems where predators are present in adequate numbers to affect prey population dynamics. Additionally, Wang et al. (2009) concluded that increased spatial heterogeneity such as diversity in slope and aspect of terrain affected potential carrying capacity of habitat for ungulates. Their review failed to observe density dependence in the most northern populations they considered, likely due to severe and variable weather plus predation effects. Highly productive systems may also be able to support high ungulate biomass in the presence of high predator numbers, as in much of the eastern white-tailed deer range (McCabe and McCabe 1997). It should be noted that KCC is rarely measured because of the time and expense of doing so (Morris and Mukherjee 2000).

The concept of variation in prey vulnerability and its effects on predation rate dates back to Leopold (1933). Boertje et al. (1996) and Hayes et al. (2003) concluded that periodic wolf control coupled with favorable weather conditions can result in higher densities of wolves, moose, and caribou than if wolf control was not conducted. This theme was expressed time and time again across the continent when investigations of predator-prey relationships were examined.

Elk, a major prey zspecies for bears, mountain lions, and wolves, reached high population levels across much of their range by the mid-1990s (Figure 1). In the 1980s, low recruitment of calves began to be noticed. One of the reasons was high hunter harvests of male elk that de-

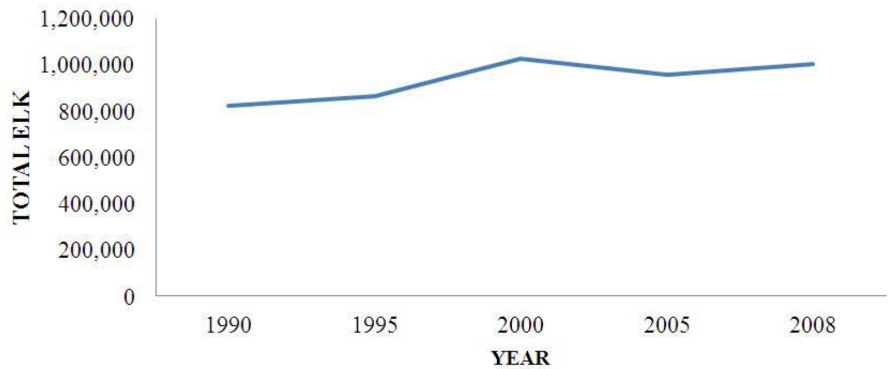

Figure 1. Elk population trends in 9 states (AZ, CA, CO, MT, NM, OR, UT, WA, WY) with more than 10,000 elk, 1990-2008.

layed breeding and reduced calf production and survival (Noyes et al. 1996). However, in most areas, adult male survival was high enough to preclude this as a reason (White et al. 2001). Shortly after these concerns were addressed, predators of elk became an issue. It would be intuitively obvious to recognize that increases in prey base to high population levels with attendant decreased reproduction and survival would not be convincing evidence that predators were the ultimate cause of these declines even if they were the proximate cause. White et al. (2010) concluded that although black bear predation was the major immediate mortality factor of elk calves in central Idaho, the habitat that influenced adult female body condition was an important factor affecting mortality. Cows in better condition produced larger calves that were less susceptible to predation. A review of the effects of bear predation on ungulates (Zager and Beecham 2006) concluded that black and brown bear predation could be important immediate causes of ungulate neonatal mortality and can have inverse density-dependent effects when ungulate populations are at low levels. However, because bears are omnivorous and prey on neonates for less than 2 months in spring, they may limit but not regulate ungulate populations (Zager and Beecham 2006).

The presence of wolves, bears, and mountain lions, as occurred prior to European settlement, probably limited ungulate populations to levels below KCC. The history of deer irruptions in the mid-1900s on the Kaibab plateau in northern Arizona (Rasmussen 1941) and other locations (Caughley 1970) occurred after predators were extirpated or reduced to very low levels, habitats were altered by livestock grazing in the earlier part of the century in ways that favored establishment and increase of major deer forage species, and soldiers leaving for World War II reduced hunting pressure. The current high populations of white-tailed deer in eastern North America occur in the absence of significant predation coupled with extensive areas where hunting is absent or seriously curtailed.

High levels of deer and elk may actually be unprecedented across much of their currently occupied habitat, given recent information suggesting that aboriginal man and predators may have kept populations at lower levels (Martin and Szuter 1999, Laliberte and Ripple 2003). In the last half of the 20th century, North Americans experienced ungulate population highs that may never be reached again, and in many cases were likely higher than during aboriginal times. In many areas, habitat degradation and loss have reduced KCC such that no amount of predator control would result in populations returning to previous highs.

Bergerud (2008) conducted an extensive review of caribou fluctuations in the Ungava region of Quebec, implicating high hunter harvests, volcanic eruptions that altered climate, weather, and starvation, and cold springs that reduced forage as causes of historical fluctuations. Recent fluctuations were attributed to variable effects of wolf predation, human harvest, and the deterioration of summer forage through different grazing pressures. The George River herd of northern Quebec-Labrador reached population highs of 700,000 in 1988, declining to 300,000 in 2001. Recruitment of calves declined from 1984 to 1990 as the population reached its high, then improved as the population declined to lower levels more in line with the carrying capacity of summer habitat. Bergerud (2008) emphasized the role of predation, particularly by wolves, as a limiting factor on caribou populations across their range, but the George River example indicates the need to consider the complex of factors that affect populations.

NEWFOUNDLAND CARIBOU: A CASE HISTORY

Predator management within the perimeter of an island ecosystem poses unique challenges and garners potential advantages that are inaccessible to continental ecosystems. Usually the numbers of predator and prey species are proportional to the size of an island, but introductions and extinctions can substantially alter systems, as has been the case in insular Newfoundland. The current predator-prey ecology of the island of Newfoundland has been shaped by several mammalian introductions, the extinction of the Newfoundland wolf (*Canis lupis beothucus*), and the recent dispersal success of coyotes.

Woodland caribou is the only ungulate native to Newfoundland and thus was a vital prey source supporting native predators in the early system. The Newfoundland wolf, until its extinction in 1922, is assumed to have been the most prevalent predator of caribou. Caribou populations undoubtedly contributed to the maintenance of black bear and Canada lynx populations on the island, but their influence on caribou population dynamics is thought to have been relatively low compared to the influence of the wolf.

Anecdotal accounts of Newfoundland caribou numbers date back to the 1800s, but systematic surveys and research did not begin until the 1950s. Comprehensive historic analysis of travel writing, newspaper articles and editorials, and other written sources indicates that the population size likely peaked at over 100,000 caribou in the late 19th century and declined rapidly to approximately 10,000 to 15,000 caribou islandwide between 1925 and 1935. Historic records from the legal hunts and local ecological knowledge suggest that the population slowly increased from the mid-1930s through the early 1950s. In the early 1950s, evidence of decreasing populations began to emerge again, followed by a period of stability until the late 1960s. The insular caribou population continued to grow slowly until about 1975 when it reached 22,500. Between the mid-1970s and the mid-1990s there was a period of rapid population growth, increasing 327% to an estimated peak of 96,300 animals in 1996. In the following years this population again experienced rapid decline (a decrease of over 67% in 14 years) to a current size of about 32,000 animals.

The wolf-caribou system that persisted until the 1920s has since been supplanted by a system comprised of a variety of predators including black bear, Canada lynx, and bald eagle *(Haliaeetus leucocephalus),* which are all native predators, and the eastern coyote, a recent arrival to the island. The coyote's arrival in the mid-1980s and subsequent expansion across the island, coincident with the recent caribou population decline, has fueled passionate debate about the future direction that predator management should take in Newfoundland. Coyotes are not the only arrival from the mainland in the past century. Among others, moose, snowshoe hare (*Lepus americanus*), red squirrel (*Tamiasciurus hudsonicus*), mink (*Mustela vison*), Eastern chipmunk (*Tamias striatus*), masked shrew (*Sorex cinereus*), and northern red-backed vole (*Clethrionomys rutilus*) were all introduced, with varying impacts on the native predator-prey system. Moose and snowshoe hare, both introduced to provide a source of fresh meat for the human population on the island, arguably had the greatest ecological consequences, altering the vertical structure of the Newfoundland forests with browsing of young trees.

Coyote in Newfoundland captured in a leg hold trap in order to collect data that will contribute to a better understanding of this predator's life history and interaction with prey and the surrounding landscape.

Moose experience a relatively low rate of predation in Newfoundland, which likely facilitated their rapid population growth and expansion across the island from 4 animals in 1904 to an estimated 120,000 by 2004. Despite low predation rates on moose, the presence of large ungulates on the island may help support higher density predator populations than would exist in their absence. Similarly, the introduction of snowshoe hare supports what is likely a larger lynx population than would exist otherwise.

Early Investigations of Caribou Mortality

Until Bergerud's (1971) work on Newfoundland's woodland caribou in the 1950s and 1960s, very little was known about the causes of caribou calf mortality. Bergerud was the first to intensively study limiting factors of Newfoundland's caribou population in an attempt to explain the slow growth of the population. This work eventually included experimental removals of lynx from 1964 to 1966 on calving areas of 2 caribou herds to test the hypothesis that lynx predation on caribou calves was limiting population growth by depressing calf survival.

When the work initiated, pregnancy rates were high (84.5% to 86%) and productivity was estimated at 94% to 96% for females 3 years of age and older. Slow population growth despite high productivity suggested that mortality of adults and/or calves was the demographic mechanism responsible for limiting population growth. Bergerud (1971) estimated adult mortality from combined natural causes and hunting (legal and illegal) to be approximately 11% island-wide from 1951 to 1961. Recruitment varied between 5.5% and 19% prior to experimental lynx control. Over-winter mortality of young was considered negligible and adult mortality was reasonably low, so calf mortality between 0 and 6 months of age was determined to be the main cause of the slow population growth of caribou.

Over the 10 years of study, mean calf mortality prior to 6 months of age was 69%. During the period prior to experimental lynx removal, early calf mortality in the interior region ranged between 58% and 85%. Predation was the determined cause of death in only 5 of 121 calf remains found (4 lynx predation, 1 black bear predation). Of the carcasses found, the majority of calves died from septicemia resulting from *Pasteurella multocida* infection delivered through saliva during unsuccessful predation attempts by lynx. Bergerud interpreted this to indicate that lynx were the major predator of neonate caribou.

To determine the importance of lynx predation, lynx removal experiments were conducted between 1964 and 1966. Forty-four lynx were trapped and removed from the Middle Ridge area and 19 were removed from the Avalon Peninsula. These trapping efforts suggested the density of lynx in Middle Ridge was approximately twice that of the Avalon Peninsula, possibly accounting for the higher calf mortality observed in the interior herd prior to lynx removal.

Following lynx removal, calf mortality was 15% in the study area and 51% in the control area, suggesting that the removal of lynx improved calf survival. In the year prior to lynx removal on the Avalon Peninsula, calf mortality was 73%; following lynx removal, calf mortality was 15%, again supporting lynx predation as a significant agent in calf mortality. Bergerud concluded that the evidence of unsuccessful predation attempts by lynx and the correlation between relative lynx abundance and differential calf mortality indicated that predation by lynx was the main mechanism for calf mortality, and hence the main cause of slow caribou population growth.

Intuitively, Bergerud's conclusions regarding the importance of lynx predation appear reasonable, but despite the attentive effort in collecting and analyzing data, there are certain weaknesses in the study which should be considered when interpreting results: (1) demographic analysis was limited by the quality of data available; (2) lynx removal experiments were of a very short duration; (3) very little was known about the predator guild or the ecology of caribou calf predators; and (4) other important factors (including body condition and habitat quality and quantity) that independently or interactively contribute to calf mortality were not considered. These weaknesses prevented determination of the importance of lynx predation as a causative factor contributing to slow population growth even in light of the removal experiments. Despite these issues, the importance of the work should not be underestimated.

Predator knowledge.— Through the pre-removal study of calf mortality, the proportion of deaths recorded resulting from successful predation attempts almost certainly underestimated the actual proportion of mortality due to predation. Calves were located without the aid of radio-collars and thus needed to be visible to be found. Predators of neonate calves leave very little of the carcass untouched and are known to sometimes bury the carcass (Mahoney et al. 1990, Norman et al. 2006), conditions that reduce carcass visibility. The evidence of unsuccessful predation attempts by lynx probably suggests high undetected mortality due to successful predation by lynx. Bergerud considered black bear to be an unimportant predator, but there was little evidence to confirm or deny this. Subsequent calf mortality studies (Mahoney et al. 1990, Norman et al. 2006) using radio-collared neonates have indicated black bear as the most prominent caribou calf predator on the island of Newfoundland.

Regardless of the relative contribution of lynx and black bear to calf mortality, Bergerud's study was conducted with little understanding of the basic ecology of either predator species. The effect of lynx removals on lynx and bear populations remains unknown. The behavioral ecology of these predators with respect to diet and prey handling remains a knowledge gap in the Newfoundland system.

Calf mortality studies in Newfoundland have been conducted regularly since 1979. In the last 30 years of these programs, the *Pasteurella* infection phenomenon cited by Bergerud has never again been recorded. Although the septicemia mortality might have led to an overestimate of the importance of lynx as a calf predator, the mortalities were real and caused by lynx, so there was something biologically unusual occurring at the time.

The Current Predator-Caribou Circumstance

At present, Newfoundland's woodland caribou are again experiencing a population decline. Demographically, as was the case prior to Bergerud's work, productivity remains within normal expectations for caribou (Mahoney and Weir 2008), adult female survival is consistent with other *Rangifer* populations across North America, and a female-biased adult sex ratio exists. Unlike conditions when Bergerud began his study, the population is not showing an increasing or stable trend. One striking similarity, however, is that early calf mortality appears to be responsible for slow population growth, and the overwhelming majority of this mortality is proximately due to predation. The predator guild on the island of Newfoundland has changed: Important predators of neonate calves still include lynx and black bear, but now have expanded to include coyote and bald eagle.

Initially, public perception placed heavy blame for the caribou decline on the coincident arrival and dispersal of coyote. There was substantial public pressure for the eradication of the coyote, an approach that has been met with little success in other parts of North America. From extensive calf mortality studies conducted since 2003, it has been determined that the coyote is not solely or primarily responsible for caribou calf mortality. It is still unknown, however, to what extent coyote predation is additive or compensatory. Calf survivorship declined dramatically, correlated with a substantial increase in predation mortality. Predation was the major cause of mortality, increasing from 59% in the 1970s to 1990s to 83% in recent years. The increased predation may be attributable to an increase in the number of predators, an increase in predator species, increased exposure of caribou to these predators, or increased vulnerability of calves to predators.

Synthesis and analysis of historic caribou data has also suggested that predation, although the main proximate cause of the population decline, may only be partially able to explain demographic and morphological trends. Density-dependent population dynamics have a greater explanatory power as an ultimate cause. Despite evidence for density-dependent decline, it is unknown whether the relief of other densi-

SCIENCE AND MANAGEMENT DIRECTIONS – THE CARIBOU STRATEGY

In 2008, the Government of Newfoundland and Labrador committed to a 5-year science and management initiative, called the Caribou Strategy, intended to address the caribou population decline through a program of inter-related research initiatives and adaptive management strategies including public engagement to increase participation in predator harvest and improve knowledge of caribou population dynamics. The research occurs primarily in 3 geographically distinct herds, allowing inter-herd comparisons. As part of this research program, a controlled and spatially explicit experiment reducing predation pressure on calves is being undertaken. The scientific research is designed and advised in collaboration with a team of academic researchers from North America. To date, 14 graduate and undergraduate students at 7 universities have been engaged in aspects of this program.

Caribou monitoring and research programs in place prior to the Caribou Strategy are continued and expanded including the herd census program and thrice annual herd composition surveys—providing vital information on caribou abundance and demographics, and the calf mortality studies in Middle Ridge and La Poile herds, expanded to include the Northern Peninsula, in which 25-30 neonate and 10-20 6-month-old calves are fitted with VHF radio collars and monitored each year in each area; more than 184 calf mortalities have been investigated. An adult collaring and monitoring program to encompass all major herds allows assessment of adult mortality rates, annual spatial behavior, and habitat associations.

The knowledge gaps in basic predator ecology in Newfoundland are being addressed through scientific study of spatial behavior, distribution and abundance, movement, and food habits. In each of the three study areas, black bear, coyote and lynx are captured and fitted with telemetry collars. One of the biggest challenges faced to date has been obtaining reliable estimates of predator abundance and density; a critical piece of information required to measure the consequence of any experimental manipulation of predator populations. The spatial coincidence of the caribou and predator studies allows for combination of data to investigate predator-prey dynamics and predator-prey-habitat interactions. Gaining a comprehensive understanding of the system is expected to provide new insights into predator-prey relationships and a solid knowledge base for developing effective management plans. Evaluating the results of this program in the context of the historic data available on Newfoundland's caribou will increase our ability to understand the role of predation and of non-predation factors influencing the caribou population.

PHOTO CREDIT: Government of Newfoundland and Labrador

This radio-collared caribou calf was killed by predators in Newfoundland. Scientists fit the calf with a radio-collar as part of study on calf mortality. Caribou in the province are preyed upon by lynx, black bears, and coyotes.

ty-dependent limitations can result in increased caribou populations given the current predation pressure on calves.

Caribou productivity has declined somewhat island-wide, although variability among herds has been observed. These herd-specific trends may reflect the differential availability of forage resources resulting in differences in female reproductive potential. Alternatively, or additionally, the high rates of early calf death from predation may have ameliorated pregnancy or productivity rates for some herds.

Indirect evidence points to deteriorated condition of caribou summer range. Compared to the early 1960s, the Buchans herd has now delayed its spring migration by 1 month, and advanced its fall migration by 1 month. This dramatic, 2-month reduction in time spent on the summer and calving range, coupled with diminished body size, implies that summer food resources are limiting. A potential consequence of nutritional stress is that females with calves may be feeding in riskier habitats where predators were more common. This suggests an intimate relationship between caribou, their food, and their predators. Available habitat could be influenced by human activity including direct habitat alteration (e.g., timber harvesting), and by induced avoidance by caribou of preferred habitat in response to human activity. While both processes represent quite different causal factors, their ultimate influence on caribou could be the same.

Despite the richness of caribou data available for this island population, there are major gaps in knowledge important for informing appropriate and effective management strategies. No comparable data exists on the population dynamics of the predator species, and other biological and ecological knowledge of these predators is relatively scant. No direct means of determining whether or how changing body and antler sizes were influencing the numerical decline are available, and measures of cause (e.g., habitat quality and abundance) and effect (e.g., changes in size, etc.), are needed. A detailed assessment of caribou range quantity and quality is required to determine if the island can currently support an increased population. The ability to effectively manage caribou and their predators depends strongly on scientific understanding of the species, their interactions, and their relationship to the landscape.

COYOTE PREDATION ON DEER

Mule deer harvest across the western states and provinces declined from 1980 to 2008 (Table 1), reflecting declines in populations. Wildlife

Table 1. Mule deer harvests in selected states (AZ, CO, ID, MT, NM, NV, OR, UT, WA, WY) and provinces (Alberta, British Columbia, Saskatchewan). The trend for AZ, CO, ID, MT, NM, OR, UT, and WY is down over the 1980-2007 period (lnTotal harvest=69.79-0.029*year, F=69.49, P=0.000, adjR2=.725).

YEAR	AZ	CO	ID	MT	NM[1]	NV	OR	UT	WA	WY	AB	BC[2]	SK
1980	11,111	54,546	36,588	57,886	18,344	10,452	56,461	75,240		54,086			
1981	10,825	67,425	40,580	64,206	23,226	13,594	31,364	90,809		58,804			
1982	12,187	75,100	37,950	73,494	25,234	11,954	37,077	85,984		66,475			
1983	12,767	78,931	38,750	98,585	19,239	11,758	32,604	95,716		64,116			
1984	17,102	64,686	30,630	112,161	20,322	11,794		67,277		52,492			
1985	16,565	58,399	36,450	74,391	22,334	19,520	34,228	64,973		52,216			
1986	19,454	52,560	46,000	60,423	21,862	21,845	41,844	67,084		50,293			
1987	17,272	59,089	51,900	62,774	25,994	21,497	41,280	74,275		47,781		27,552	
1988	15,525	70,383	62,746	74,226	19,053	26,784	43,328	90,738		53,482		29,926	
1989	14,210	79,749	72,410	77,400	15,729	17,782	25,985	78,373		60,416		29,004	
1990	14,087	90,490	51,874	83,633	18,329	16,715	36,688	75,783		68,099		32,125	
1991	12,101	79,384	42,223	87,122	15,020	12,442	35,326	66,876		81,277		32,544	
1992	11,997	73,955	41,404	94,779	17,863	14,273	38,714	69,665		87,010		33,329	
1993	11,879	61,515	24,747	85,570	16,888	6,276	18,023	30,320		58,336	15,897	25,686	
1994	10,867	54,818	24,432	91,445	13,273	7,315	28,315	29,926		36,011	17,836	24,551	
1995	8,824	52,144	21,191	76,229	11,966	8,114	28,466	27,830		31,935	19,162	22,829	
1996	7,229	55,873	24,346	55,366	14,249	11,070	29,581	37,159		29,487	17,528	18,938	
1997	6,065	45,468	21,174	47,429	12,928	8,263	37,862	33,046		26,697		17,154	
1998	5,877	41,539	20,419	42,718	14,486	9,672	36,735	35,088		29,990		17,111	
1999	5,924	29,639	24,650	45,681	14,363	11,020	34,503	34,433		39,652		14,669	
2000	5,213	37,908	25,100	56,155	13,045	12,499	33,217	37,551		43,544		15,541	
2001	5,849	31,634	23,400	60,613	10,402	9,791	32,623	31,663	11,915	38,305		18,812	
2002	4,540	36,075	23,070	62,888	8,431	6,899	29,646	27,508	13,639	37,580		16,654	
2003	3,753	37,682	25,937	67,845	8,023	5,982	28,173	25,049	13,280	35,382		19,605	
2004	4,037	41,743	25,934	64,854	6,681	6,560	21,453	30,168	13,964	36,733		15,825	
2005	4,357	41,665	30,874	56,112	9,336	7,112	28,039	23,471	12,638	35,266		24,018	
2006	4,811	44,784	28,560	66,269	8,562	8,346	24,136	32,404	10,074	40,067		22,243	
2007	5,388	45,026		68,484	12,256	8,743		32,308	10,421	41,106		22,557	
2008		35,552		63,993	11,112						17,730	22,074	

[1] NM estimates are .93* total harvest of both deer species.

[2] BC estimates 1987-2006 for resident hunters.

agencies changed regulations to increase adult male survival and reduce female harvest between 1980 and 2007. For example, Colorado limited male deer hunting licenses after 1998. Severe winters, prolonged drought, deteriorating habitat, and predation were reported as reasons for the decline (Mule Deer Working Group 2004).

Low survival of fawns prompted an experimental investigation into the role of predation on depressing populations (Bartmann et al.

1992). Subsequently, Ballard et al. (2001) reviewed 25 investigations including 15 on mule deer, 2 on black-tailed deer (*Odocoileus hemionus)*, and 7 on white-tailed deer, which yielded insights on the effects of predation relative to deer density and to KCC, and on whether the mortality was compensatory or additive. Most studies were short term, conducted in relatively small areas, with only a few demonstrating increases in fawn recruitment and subsequent increases in harvest by humans after predator reductions. Conditions leading to predation limiting deer populations were poorly documented. A number of related factors, including other predators, alternative prey species, human harvest, and density in relation to KCC needed better examination.

When deer populations were lower than levels approaching KCC, predator reductions were more likely to result in increases in survival and numbers (Table 2). Investigations into the timing of mortalities were then needed to determine when reductions in predators would have the greatest influence on prey. Ballard et al. (2001) concluded that large losses immedi-

Table 2. Summary of investigations reviewed by Ballard et al. (2001) on predation effects on mule deer, black-tailed deer, and white-tailed deer.

No. of Studies	Predators Involved	Were Predators Reduced?	Relation of Deer to KCC[1]	Type of Mortality
MULE DEER				
10	Coyote	Yes in 4	Below-2	Additive-2
	Coyote		At-2	Compensatory-2
	Coyote	No in 6	At-2	Compensatory-2
	Lion		Below-2	Additive-1
	Coyote			Additive+Compensatory-1
	Coyote		UNK-2	Additive-2
BLACK-TAILED DEER				
2	Wolf, Lion	Yes	Below	Additive
	Wolf	No	At	Additive
WHITE-TAILED DEER				
7	Coyote	Yes in 3	Below-2	Additive-2
	Coyote		At-1	Compensatory-1
	Coyote	No in 2	Below-2	Additive-2
	Wolf			Compensatory-2
	Coyote, Bobcat	UNK-2	Above-1	Compensatory-1
	Coyote		Below-2	Additive-1

[1]KCC is the estimated food-based carrying capacity.

ately following parturition suggest predation was responsible. These findings allowed managers to decide on the scale of control needed and when control should occur. In addition, their review provided evidence that reductions in predators followed by increases in deer populations at or above KCC could result in forage plants being browsed or grazed at high levels with subsequent habitat deterioration, causing a reduction in productivity and condition of the deer. If predators were to be reduced, then hunter harvest needed to be intensive enough to maintain deer populations and habitats at productive levels.

Coyote control was effective at increasing deer populations when deer were below KCC and (1) predation was the limiting factor, (2) predators were reduced enough to yield results, (3) control efforts were timed to be most effective, and (4) the control was confined to a limited area. Predator control was not effective when deer populations were near KCC, predation was not limiting, predators were not reduced enough, and the control was practiced over a broad area (Ballard et al. 2001).

Collinge (2008) estimated a population of 50,000 coyotes in Idaho. The U.S. Department of Agriculture (USDA) Wildlife Services in Idaho killed an average of 5,134 per year from 1980 to 2006, or just over 10% of the estimated population annually. Coyote control was not limiting the statewide population, even if it may have been effective in reducing depredations of livestock.

Wagner (1988) reasoned that the number of coyotes killed in efforts conducted by USDA Wildlife Services to reduce their depredations, primarily on livestock, fluctuated in accordance with coyote population levels. There are no trends in coyote population indices for western states between 1970 and 1980, and the total annual kill from 1998 to 2008 averaged 83,000 coyotes with no apparent trend. The total annual kill in 12 western states accounted for 83% nationwide with no apparent trend from 1990 to 2007 (Table 3). These records likely reflected trends in populations, assuming the amount of effort and the nature of the operations were relatively constant over time, but other factors such as changing livestock management practices were involved. Declines in southern states reflected the prolonged drought that reduced prevalence of livestock on control areas and reduced the need for coyote control. Changes in coyote populations farther north could be attributed to changes in natural forage as well as to populations of rodents and ungulates (Hamlin et al. 1984, Hurley et al. 2011). No consistent relationship exists between data and the overall trends in mule deer populations in western states (Hamlin et al. 1984, Bishop et al. 2009, Hurley et al. 2011). While mule deer were generally declining to lower levels, coyote control numbers declined in 4 states, were stable in 5 states, and were up in 2 states. These observations suggested that large-scale changes in mule deer numbers and coyote kill were not reflective of local influences of coyotes on mule deer. Attempts to reduce coyote levels in local areas were not likely to influence overall levels of mule deer harvest at the state level.

Wagner (1988) concluded that local control of coyotes and nonlethal preventive control at local levels were effective in reducing depredations on domestic lambs and ewes, but that attempts at region-wide suppression of coyote populations were less effective. Efforts to reduce predation on game animals would also be most effective at local levels rather than region-wide.

An evaluation of the efficacy of broad-scale coyote control for purposes of reducing livestock depredations needs to be conducted (Mitchell et al. 2004). Palmer et al. (2010) reported that 4.9% of lambs were killed by predators in 2006 and 2007, compared to 9.5% killed by predators between 1972 and 1975 on Cedar Mountain, Utah, where predator control was present in both periods. Increased predation by mountain lions and black bears and reduced levels of predation by coyotes were noted in more recent time when compared with the earlier investigation, indicating a potential reason for the increased rates of predation by these species. Changes in predator populations and livestock management all relate to levels of predation of livestock.

Table 3. Coyote harvests by USDA APHIS Wildlife Services by all methods, 1990-2007, for 12 states that constitute 83% of the total kill.

YEAR	AZ	CA	CO	ID	MT	NM	NV	OR	TX	UT	WA	WY	TOTAL
1990	1,503	7,697	3,261	3,952	7,438	6,763	6,593	6,001	18,573	4,165	458	7,320	73,724
1991	1,528	5,926	2,094	5,333	5,038	7,456	5,833	7,664	17,807	4,347	2,375	5,911	71,312
1992	1,810	7,552	3,753	5,506	8,720	7,154	6,124	7,442	19,255	4,444	565	5,483	77,808
1993	1,577	7,307	2,339	4,546	6,815	8,252	4,386	6,842	19,913	4,932	3,313	5,829	76,051
1994	1,880	7,317	3,662	4,012	6,328	6,263	3,870	8,698	20,877	3,142	3,179	5,302	74,530
1995	1,984	5,549	3,169	3,160	7,079	7,173	6,226	8,189	18,551	5,827	2,760	7,873	77,540
1996	1,919	1,651	2,101	8,155	5,333	6,134	5,621	6,231	17,377	4,421	690	5,021	64,654
1997	1,525	8,786	2,423	6,423	8,118	5,128	5,433	6,593	14,148	4,728	596	7,286	71,187
1998	940	8,390	3,088	4,135	8,458	6,213	4,014	5,996	16,223	4,169	898	6,144	68,668
1999	520	7,361	5,155	4,654	9,506	7,269	4,327	5,471	17,753	4,412	147	6,442	73,017
2000	869	8,714	3,351	5,471	9,606	6,132	7,013	6,203	16,602	4,534	1,466	6,174	76,135
2001	950	8,319	3,525	5,113	9,964	6,025	5,978	5,997	17,540	4,275	1,197	7,857	76,740
2002	821	7,354	3,308	5,655	9,905	6,122	4,825	5,689	18,807	3,874	679	6,689	73,728
2003	774	6,165	2,408	4,332	8,013	5,402	4,795	4,058	18,136	3,394	292	6,029	63,798
2004	861	6,347	2,705	5,376	9,751	5,388	5,728	3,811	16,702	3,897	153	6,258	66,977
2005	907	6,103	2,924	3,610	6,483	4,350	5,367	4,254	16,704	4,166	114	6,444	61,426
2006	1,093	6,268	2,919	8,285	8,615	4,370	6,651	5,602	19,864	4,798	585	7,860	76,910
2007	1,218	7,759	2,738	4,690	8,851	4,564	7,447	6,491	19,117	4,888	608	9,432	77,803
TOTAL	21,461	116,806	52,185	87,718	135,170	105,594	92,784	104,741	304,832	73,525	19,467	109,922	1,302,008
MEAN	1,262	6,871	3,070	5,160	7,951	6,211	5,458	6,161	17,931	4,325	1,145	6,466	

Coyotes have recently increased across the eastern part of the continent (Hill et al. 1987). In Virginia, populations were established in the late 1970s and now occur across the entire state (M. Fies, 2009, personal communication). Coyotes also now occur in all southeastern states (Hill et al. 1987), noticed in initially in the late 1940s in Louisiana and in the 1960s in Arkansas. Releases of coyotes for chase with hounds and escape of captive coyotes augmented natural establishment.

Coyotes (also called "brush wolves" or "tweed wolves") were initially recorded in western Ontario at the beginning of the 20th century (Ontario Ministry of Natural Resources 2004). DNA profiles of coyotes in Ontario today indicate they are actually hybrids of eastern wolves and coyotes (Wilson et al. 2000). The coyote harvest for fur (Statistics Canada 2008) also reflects their expansion in eastern Canada. Prince Edward Island recorded pelt sales starting in 1983, with between 0 and 5 pelts sold annually through 1989. Pelt sales in Nova Scotia increased from 17 in 1980 to an average of 2,081 from 2002 to 2008. Pelt sales in New Brunswick also indicated a generally increasing population.

Coyote pelt sales for all provinces fluctuated without any trend from 1980 to 2006. However, in contrast to the eastern provinces, a decline in reported total harvest for the 4 western provinces was evident (Table 4). The trend was similar to reduced harvest of ungulates in these provinces and likely did not reflect declining coyote populations. Harvest dropped from between 43,000 to 51,000 pelts to just over 12,000 pelts in the late 1980s, then increased in 1992 and fluctuated around 28,000 pelts through 2006. The mean price per pelt was significantly cor-

Table 4. Coyote take as fur in 9 Canadian Provinces (Alberta, British Columbia, Manitoba, New Brunswick, Newfoundland, Ontario, Prince Edward Island, Quebec, Saskatchewan), 1980-2008.

YEAR	AB	BC	MB	NB	NL[1]	ON	PEI	QC	SK	PELT TOTAL
1980	20,986	2,949	4,995	368		2,640			12,863	44,801
1981	31,652	4,018	7,438	496		2,784			19,815	66,203
1982	37,447	3,506	9,992	797		2,347			19,059	73,148
1983	31,445	4,081	8,569	755		3,946	1	1,991	15,677	66,465
1984	37,654	3,460	10,400	1,132		2,603	0	2,413	25,446	83,108
1985	29,062	2,783	9,000	1,379		2,579	1	2,709	17,688	65,201
1986	35,730	3,872	11,148	1,286		2,697	0	2,741	21,159	78,633
1987	33,839	3,482	8,767	1,633		2,288	1	3,181	18,648	71,839
1988	13,234	1,081	2,971	645		1,553	2	2,242	8,902	30,630
1989	10,201	577	2,431	510		1,092	5	2,100	5,418	22,334
1990	11,886	566	2,766	239	2	1,312	17	1,722	5,128	23,638
1991	19,885	1,043	4,421	788	2	2,913	26	4,086	9,586	42,750
1992	25,965	1,613	4,169	948	8	3,096	95	3,866	7,598	47,358
1993	25,901	963	3,749	1,126	7	4,335	131	3,014	8,417	47,643
1994	26,719	1,496	2,713	1,163	2	3,465	177	2,635	9,815	48,185
1995	21,286	1,295	2,031	1,098	3	3,758	205	2,037	8,276	39,989
1996	30,687	966	2,836	1,373	5	3,842	247	2,629	14,919	57,504
1997	31,650	1,030	2,620	814	5	1,991	242	2,104	9,058	49,514
1998	21,682	804	1,820	753	15	1,561	154	2,163	8,472	37,424
1999	21,022	704	2,401	1,095	17	1,339	263	2,975	13,339	43,155
2000	24,861	651	3,780	1,293	24	1,463	403	3,245	18,187	53,907
2001	21,231	982	4,537	1,893	55	1,442	459	4,304	18,843	53,746
2002	25,554	1,324	7,890	2,025	105	1,857	470	4,765	32,351	76,341
2003	28,590	1,188	8,376	2,581	375	1,923	479	4,233	35,511	83,256
2004	27,402	1,228	7,968	1,920	405	2,215	344	5,007	19,597	66,086
2005	28,807	1,369	8,566	2,229	541	2,421	236	4,961	16,515	65,645
2006	28,921	1,580	9,730	2,478	634	3,055	397	6,855	28,803	82,453
2007		1,206		1,150		3,062	368	4,116		
2008		846		1,574		2,136	416	5,225		

[1]Values not listed for NL, NS, and PEI

[2] Values scaled to 2008 CDN

related with total harvest (Figure 2), similar to experiences in the western U.S. (Wagner 1988). Coyote pelt prices for all provinces ranged from 16.05 to over 65.59 CAD per pelt from 1980 to 2006. The recorded harvest corroborated conventional thought that region-wide coyote populations were not materially affected by human harvest and economic considerations had a major influence on harvest.

Maine Coyote and Deer Investigations

Coyotes have been killed for 37 years in Maine in an effort to reduce predation on wintering deer (Figure 3). The Maine Department of Inland Fish and Wildlife (MDIFW) provided legal (and liberalized) opportunities to hunt and trap coyotes for decades. Hunters and trappers have adopted new strategies to remove coyotes

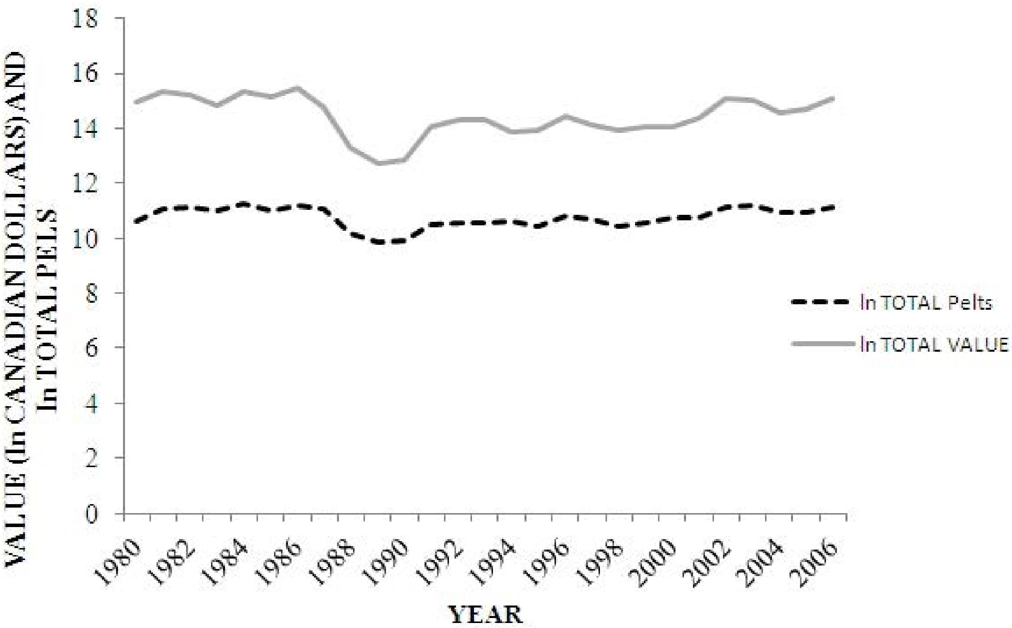

Figure 2. Coyote pelt numbers and values (CAD) for 4 Canadian Provinces (Alberta, British Columbia, Manitoba, Saskatchewan), 1980-2006 (Statistics Canada 2006).

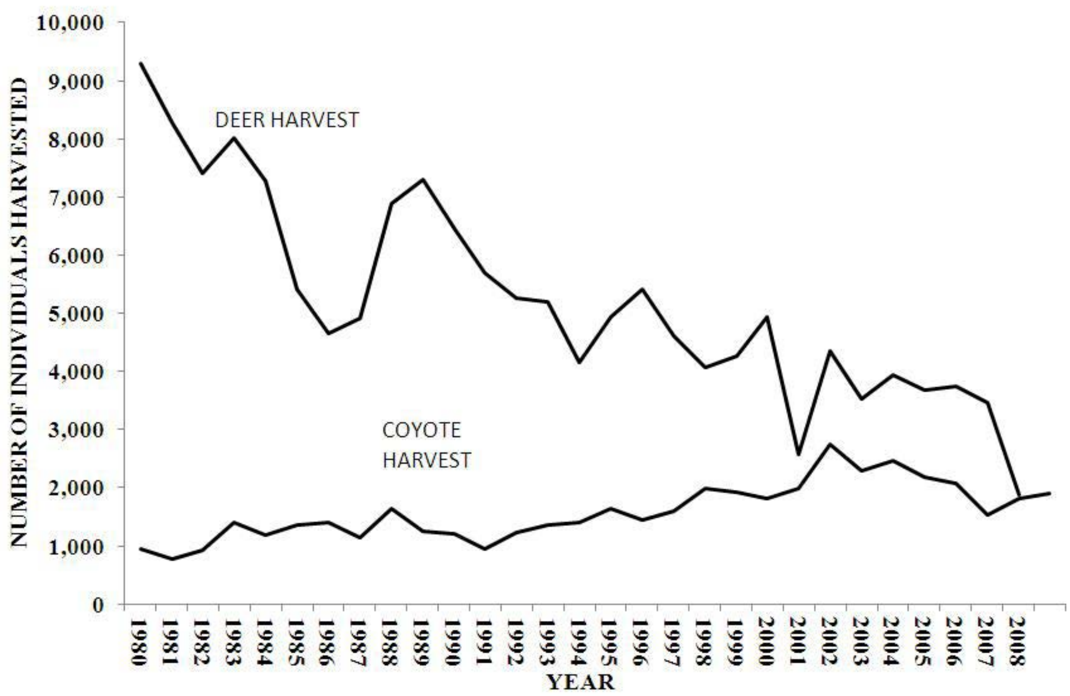

Figure 3. Deer harvests in 11 northern hunting units and statewide coyote harvest in Maine, 1980-2008.

with high success in limited areas, taking large numbers by shooting over bait as well as by running coyotes with dogs. Abundant recreational opportunities occurred but outcomes were poorly understood.

In northern Maine, the quality of deer wintering areas has been reduced by logging, natural disturbance, and aging of stands. Deer wintering areas undergo heavy forage use when deep snows concentrate deer in winter cover for 3 to 4 months. The combination of concentrated deer densities and low browse availability promoted declines in wintering area quality over time. Browse surveys (Potvin and Gosselin 1995) in the Moosehead region of Maine suggested that browsing intensity was at high levels and that available habitat would not support many deer during moderate to severe winter conditions. These circumstances promoted mortality among white-tailed deer even without predation.

Coyote predation on white-tailed deer was considered additive during wintering conditions when predation was non-selective (Lavigne 1992) and during fawning when adult coyotes were provisioning pups (Jakubas 1999). Prior to the 1970s, coyotes were likely not viewed as they are now because populations have increased and their range has expanded. In 1971, coyotes were classified as furbearers and trapping was allowed. Two years later, hunting and trapping of coyotes was legal year-round and not limited until the 1976 to 1977 season (Jakubas 1999). Initial "predator control" activities occurred in 1979 to 1980 when MDIFW initiated a coyote control policy to limit losses of white-tailed deer and other wildlife species. Under this policy, agency personnel were responsible for selecting and directing licensed trappers to trap or snare coyotes around deer wintering areas where it was determined that coyotes were exploiting aggregated deer.

Recreational coyote hunting and trapping was soon modified to include year-round general hunting, a special night-hunting season (January to June), coyote trapping during the general trapping season (generally late October through late December), and an early coyote/fox trapping season (generally 2 weeks during mid- to late-October). Coyote control that started in the 1979 to 1980 season was altered 3 years later when MDIFW established a formal damage control program in 1983. An Animal Damage Control (ADC) Coordinator position was created in the Wildlife Division and was further refined in 1989. Certified ADC cooperators were authorized to set neck snares for coyotes near deer yards where predation was deemed a problem by MDIFW officials. Snaring guidelines included safeguards against accidental catches of non-target animals such as bald eagles and deer. The policy was revised in 1998 to increase training and incentives for ADC snarers, modify equipment requirements, allow experienced snarers more snaring opportunities, and increase MDIFW monitoring and control of snaring activities (Jakubas 1999).

In 2007, concerns regarding decreasing deer densities in northern Maine increased to a level that precipitated legislative bills and a Northern and Eastern Maine Deer Task Force was developed by the Commissioner of MDIFW. The task force was charged to characterize the status and condition of the deer population in northern and eastern Maine, review ways to enhance deer wintering, review coyote management policies, and submit "workable" recommendations. The task force was composed of representatives from MDIFW, the forest industry, sportsmen, small woodlot owners, the Audubon Society, and professional guides.

After review of the report in 2008, the Legislature's Joint Standing Committee on Inland Fisheries and Wildlife passed LD 2288 (Resolve, To Create a Deer Predation Working Group). The periodic involvement and extent of actions by stakeholders and the relative intensity of debated issues influences management direction. Given gaps in knowledge of the relationships between habitat, predation, and productivity/recruitment, use of the best available data to inform decision-making with an objective of adhering to scientifically-derived information is preferred. Public involvement remains an important check on government management of the resource and is firmly entrenched within Maine's system of managing wildlife.

To date, no studies have been conducted to evaluate the effectiveness of coyote snaring in Maine. Snaring efforts and incidental harvest monitoring occurred for one year during snaring, and the number of participants in the program was low. MDIFW's work on the dynamics of winter severity, deer mortality, and coyote predation has demonstrated that in hard winters coyotes kill deer non-selectively (Lavigne 1992). Additional research from other jurisdictions indicated that coyotes provision their young in the early summer with deer meat, and this may be a significant factor in decreasing deer recruitment (Ballard et al. 1999). Knowledge of the potential breakdown of coyote territoriality and changes in pack structure due to harvest is lacking, as is knowledge on how changes in the social dynamics of coyotes may alter predation pressure on wintering deer. It is generally accepted that control of coyotes at the landscape level has not been effective in increasing deer densities, but localized control may be effective in promoting deer population growth.

Since 2005, deer numbers in northern and eastern Maine have continued a downward slide in some areas while stabilizing or slightly increasing in others. In the southern reaches of the state, deer numbers are currently at target densities. Deer can be managed in southern and central areas using antlerless deer permits in relation to district density objectives and by adjusting permit levels due to winter severity, previous doe harvest success, skewed adult sex ratios, and relative balance of mortality with recruitment. However in northern and eastern Maine, deer numbers have not responded to "bucks only" seasons, and the continued combination of marginal habitat, predation, and poor recruitment has stagnated population growth. Ultimately the relationship between coyotes and deer and their relative population levels will be dictated by ecological and sociological factors.

MOUNTAIN LION MANAGEMENT

Mountain lion management is directed extensively by public sentiment (Hornocker 2009).

> Consider the following example of how public perceptions influence mountain lion management. In February 2009, a lion was shot in Ashland, Oregon because it was thought to be killing neighborhood pets. Rumors that pet collars were found in its stomach turned out to be untrue and resulted in an apology from the law enforcement people that spread the rumor (Associated Press, 22 February 2009).

When ungulate hunters fear that predation on game is high enough to impede hunter success, state wildlife agencies respond to those fears by liberalizing harvest regulations for predators. However, mountain lion hunters may also demand that harvests be reduced if they perceive that their sport (hunting mountain lions with the use of dogs) is jeopardized by high harvest levels (Curtis and Dickson 2008). Non-hunters that either fear attacks by mountain lions or are concerned with protecting them will also have an influence on harvest, distribution, and numbers. Further, the dispersed nature of residences in open country—where substantial populations of deer and other prey occur and hunting of deer and mountain lions is prohibited—can provide corridors for movement and suitable habitat (Markovchick-Nicholls et al. 2007, Morrison and Boyce 2008).

Lambert et al. (2006) concluded that mountain lion populations in the Pacific Northwest, including northern Idaho, Washington, and southern British Columbia, were declining. Increased conflicts can result from a reduction in age structure of the population caused by heavy hunting, increased human intrusion into mountain lion habitat, low levels of social acceptance of mountain lions in an area, and habituation of mountain lions to humans. Lambert et al. (2006) recommended reductions in harvest, especially of adult females, continuous monitoring, and better collaboration between managers across the region.

Investigations in Utah reported that harvests of mountain lions that exceeded 40% of the adult population resulted in precipitous population declines of over 60% (Stoner et al. 2006). Annual harvests of over 30% were considered sufficient to reduce density, fecundity, and age structures. Recovery of populations that were harvested at these high levels could be very slow, although immigration of individuals to the affected areas may hasten increases.

Robinson et al. (2008) provided information that mountain lion harvests in game management areas of 1,000 km^2 or less could result in little or no reduction in local mountain lion densities and a shift in population structure toward younger animals. Hunting in these small areas of high-quality habitat may create an attractive sink, leading to misinterpretation of population trends and masking population declines in the sink and surrounding source areas. However, reductions of mountain lions in larger areas may preclude immigration and depress populations. Cooley et al. (2009) concluded that lightly hunted mountain lion populations in Washington study areas constituted source populations showing considerable emigration to other areas and did not result in increased production/survival and densities of the study populations.

Breitenmoser et al. (2005) reported that although interactions between mountain lions and humans remained at less than one attack per year, such attacks on humans have strong emotional connections in local communities and require further understanding of public fear and risk perception. On the basis of an examination of newspaper coverage of this species from 1985 to 1995, Wolch et al. (1997) suggested that attitudes of Californians towards mountain lions were changing to support management. During that time, sport hunting of this species was banned.

Other research specific to the southwestern U.S. was very focused in context. Casey et al. (2005) reported local support of mountain lion conservation among Arizona residents living near Saguaro National Park. Respondents overwhelmingly supported management to protect mountain lions and opposed measures removing protections. Utah residents were questioned about controversial practices of mountain lion hunting in their state and disapproved of some management strategies for the species. Teel et al. (2002) reported that residents disapproved of using hounds to hunt mountain lions, but rural residents, men, those of lower education, hunters, and long-term residents of the state were most supportive of hunting the species. Women disapproved strongly of all predator management practices in that survey.

Residents from 6 southwest Oregon counties illustrated the conflicting public opinions about mountain lions (Chinitz 2002). Oregonians predominantly supported a robust mountain lion population and believed occasional contact with mountain lions is a part of living in the Pacific Northwest. However, respondents strongly supported the right to kill a mountain lion that was a threat, regardless of governmental regulations. A similar survey of Washington residents reported very high support for reduction of predators when human safety was an issue (Duda et al. 2002). Zinn and Manfredo (1996) reported that Colorado residents felt mountain lions coming into residential areas along the Front Range needed to be controlled.

Mountain lion management received extensive political involvement in California, Oregon, and Washington. Mountain lion hunting was prohibited in 1972 in California (Updike 2005). A voter initiative (Proposition 117, passed in 1990) designated the mountain lion as a specially protected mammal. From 1997 to 2004, a total of 3,930 incidents involving humans and lions (an average of 491 per year), have been recorded. Of these incidents, 93 were considered serious (an average of 11.5 per year), resulting in 78 lions killed (an average of 9.75 per year). The California experience illustrated that simply stopping the hunting of mountain lions did not curtail mortality and may increase the number of interactions between humans, property, and mountain lions.

A ballot measure in 1994 prohibited the use of dogs in taking mountain lions in Oregon, with a resulting drop in harvest the following 2 years (Oregon Department of Fish and Wildlife 2006). Prior to 1995 and the prohibition, the mean number of non-hunting mortalities averaged 23.3 mountain lions per year. Following the prohibition, the mean number of non-hunting mortalities increased to 116.2 mountain lions per year. Statewide hunter harvest for the 9 years preceding the prohibition (1986-1994) averaged 151.1 per year (range 117 to 187). After the prohibition, from 1995 to 2003, hunter harvest averaged 141.9, with increases in the harvest from a low of 34 in 1995 to a high of 241 in 2003. The increases were considered attributable to concerns for human safety, pets, and depredations on livestock, plus increased interest in hunting.

The Washington prohibition resulted from state initiative I655 that was passed by voters in November 1996. Subsequently, heavy political pressures in 5 sparsely populated northeastern counties led to the creation of a pilot program to control mountain lion populations in those counties using dogs. This became law in March 2004. Kertson (2005) reported that 138 stories concerning mountain lions were either televised or published in newspapers from 2000 to 2004. The objective for mountain lion management in this area was to reduce populations to minimize threats to public safety and property, as well as to manage healthy, productive populations (Beausoleil et al. 2005). The west coast experience illustrates the conflicts and results of political intervention in mountain lion management, which included unintended consequences.

Mountain lion harvests for the provinces and states have changed over the past 2 decades (Table 5). The harvest in jurisdictions other than California, Oregon, and Washington increased to a high in 1997 and has declined since (Figure 4). This trend was most pronounced in British Columbia, Idaho, Montana, and Utah, which had the highest harvests, and influenced the overall trend. The harvest in New Mexico, Nevada, and Wyoming generally increased from 1990 to 2007, and the harvest in Arizona and Colorado generally leveled off by the mid-1990s. Anderson et al. (2009) concluded that mountain lion populations were declining in British Columbia, Idaho, and Washington, increasing in Oregon and South Dakota, and stable in California and Nevada.

Mountain lion management guidelines (Beck et al. 2006) have been a source of concern for wildlife agency administrators (Shroufe 2006, Mansfield 2009) because they have not effectively addressed the stakeholder values and the legal mandates that state wildlife agencies must deal with. For example, in western Montana, mountain lions increased from the 1970s to the mid-1990s, and hunting also increased (Williams 2005). When nonresident hunters increased, pressures were brought on the Montana legislature that resulted in a law that reduced harvests that were higher than designated quotas, and also reduced nonresident hunting. Hunting mountain lions in the northwestern region of Montana became more popular in the 1990s, which resulted in reduced numbers of animals over 3 years of age in the harvest. A permit-only system was established in 2005, which resulted in an increasing harvest of these older animals as populations increased and hunters became more selective (Vore 2010). Establishment of quotas and permits for each hunting unit with a subquota for females has resulted in a more acceptable hunt for participants.

Information from the Salmon River region in central Idaho provided another example of how perceptions affect management of mountain lions. The 1986 to 1990 mountain lion management plan for this region (Power and Hemker 1985) stated that mountain lion populations were not heavily harvested because of limited access. The management goal was to maintain existing populations and harvest and recreational opportunities, and to encourage harvest of males rather than females. The plan stated that harvest of the youngest age class (3 years and younger) should average below 25% of the total harvest. Lindzey (1987) reported that minimizing harvest of females would likely reduce orphaning of juvenile mountain lions.

The next Idaho Mountain Lion Management Plan (Rachael and Nadeau 2002) revised the objectives of management in response to sportsmen's concerns about declining ungulate

Table 5. Mountain lion harvests in western North America with comparative harvests from Alberta and British Columbia, Canada, 1990-2007.

YEAR	AZ[1]	CA[2]	CO[3]	ID[4]	MT[5]	NM[6]	NV[7]	OR[8]	TX[9]	UT[10]	WA[11]	WY[12]	Totals[13]	AB	BC
1990	229		235	352	227	108	88	201	35	217	102	65	1,521	48	204
1991	205		228	171	236	119	125	124	22	265	120	50	1,399	40	151
1992	234		295	330	357	105	150	184	41	241	140	75	1,787	55	197
1993	238		299	450	424	127	173	162	40	372	121	80	2,163	62	207
1994	256		330	450	566	150	161	199	46	352	177	90	2,355	54	279
1995	266		314	700	535	119	134	22	47	431	283	110	2,609	62	235
1996	265		391	635	567	177	143	43	45	452	178	140	2,770	59	387
1997	320		419	834	728	168	210	61	50	576	132	145	3,400	77	304
1998	342		407	804	776	153	178	110	46	492	184	170	3,322	97	358
1999	298		337	652	654	156	149	169	33	373	273	205	2,824	110	326
2000	329	7	317	728	584	236	224	188	27	435	208	175	3,028	107	325
2001	384	11	439	628	509	214	193	220	43	449	220	210	3,026	83	253
2002	319	13	372	514	407	192	144	232	56	406	136	200	2,554	101	218
2003	296	2	370	569	346	242	227	249	88	427	147	200	2,677	79	171
2004	279	12	336	459	335	194	136	264	35	448	191	180	2,367	103	146
2005	245	7	238	466	322	140	145	221	23	321	187	178	2,055	82	116
2006	262	11	482	480	287	224	169	289	33	339	184	186	2,429	112	151
2007	283	12	295	450	309		189		31	291	172	224	2,041	119	

1 Arizona Game and Fish department. 2008. Hunt Arizona. Survey Harvest and hunt data for big and small game. 188 pp.

2 Updike, D. California Mountain Lion Status Report. California Department of Fish and Game, Sacramento.

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4 Nadeau, S. ed. 2007. Mountain Lion. Idaho Dep Fish & Game progress report W170R31. 121pp. Boise.

5 Giddings, Brian. 2008 pers. commun. Montana Fish, Wildlife & Parks, Helena.

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8 Oregon Department of Fish and Wildlife. 2007. Big Game Statistics. Pp 111. Salem.

9 Richardson, C. 2008, pers. commun. Texas Parks & Wildlife. Midland. Recorded sport harvest only.

10 Hersey, K.R. et al. 2008. Utah cougar annual report 2006 and 2007. Publication 08-35. Utah Division of Wildlife Resources

11 Hornocker, M., and S. Negri. 2009. Cougar Ecology & Conservation. Appendix 2. Univ. Chicago Press.

12 Wyoming Game & Fish Dep. 2008. Annual mountain lion mortality summary. Lander. 2006 Mountain lion management plan

13 AZ, CO, ID, MT, NM, NV, UT, WY Only

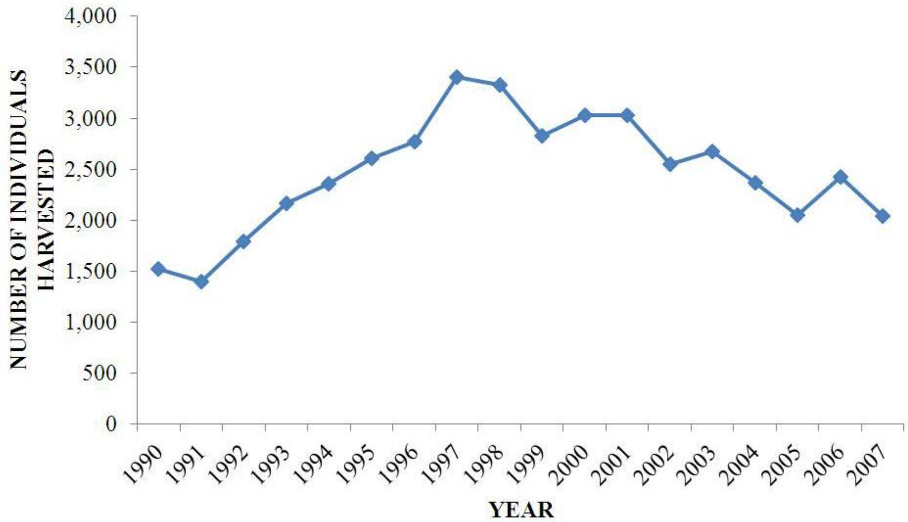

Figure 4. Mountain lion harvest for Arizona, British Columbia, Colorado, Idaho, Montana, New Mexico, Nevada, Utah, and Wyoming – all jurisdictions without constraints on hunting including prohibiting use of dogs or outright elimination of harvest, 1990-2007.

recruitment. Much of the mountain lion hunting in this area was done by guide-outfitters, who exert major influence on wildlife management. Two-lion bag limits were implemented in this area, with hunting seasons extending from August 30 to April 30. The Idaho Fish and Game Commission's intent in this plan was to maintain current distribution of mountain lions throughout the state and to maintain current levels of recreational opportunity for hunting, but not to maintain existing populations as the earlier plan stated. The management directive was changed to "sufficient management flexibility to regulate lion densities as appropriate for specific areas." Lion hunting opportunity was increased, particularly where lions were perceived to be negatively affecting elk and deer populations.

The 2002 plan (Rachael and Nadeau 2002) recognized that a period of 3 to 5 years was required to recognize harvest trends. Subsequently, Anderson and Lindzey (2005) reported that as lion populations were harvested more intensively, proportions of younger animals and females would increase in the harvest. Anderson and Lindzey (2005) reported that mountain lion populations did not begin to decline until adult (3 years of age or older) females comprised at least 25% of the harvest. Population simulations provided by Packer et al. (2009) suggest that when no male mountain lions over 4 years of age occur, populations may be expected to decline.

An analysis of 3-year running averages from 1994-1996 through 2004-2006 (Table 6) shows that the percent of females in the harvest from 1994-1996 to 1997-1999 averaged 33% (range 27-42%). The percent of females harvested from 1998-2000 through 2003-2005 averaged 52.3% (range 50-56%). The 2004-2006 average dropped to 38% females. For the 2003-2005 years, the age composition was 29% adult females (range 0-58%), 12% sub-adult females (range 8-18%), 49% adult males (range 24-87%), and 10% sub-adult males < 3 years old (range 0-25%). The total number of sub-adults of both sexes in the harvest was 22%, just under the 25% considered allowable under the 1986-1990 plan.

In the meantime, the elk population that was thought to be receiving heavy predation had reached all-time recorded highs by the early 1990s in this area, and calf production and survival had begun to drop. While predation levels may have increased along with the elk

Table 6. Sex composition of the mountain lion harvests in hunting units 20A, 26 and 27 in Frank Church River-of-No-Return Wilderness and adjacent areas of limited access in central Idaho, using 3-year averages (Nadeau 2007a, Power and Hemker 1985, Rachael and Nadeau 2002).

YEARS	# ♀♀	# ♂♂	TOTAL	% ♂♂
1994-1996	18	62	80	29
1995-1997	24	90	114	27
1996-1998	37	108	145	34
1997-1999	50	120	170	42
Average 1994-1999: 33% ♀♀				
1998-2000	59	113	172	52
1999-2001	59	106	165	56
200-2002	44	86	130	51
2001-2003	38	72	110	53
2002-2004	25	50	75	50
2003-2005	27	52	79	52
Average 1998-2005: 52% ♀♀				
2004-2006	21	55	76	38

population, a decline in calf production/survival would have occurred as the high numbers of elk began to interact more with the forage base and with winter severity, and as the age structure of adult females lengthened. Attempts to maintain high calf production and survival at high population levels by reducing mortality had acted in reverse to what was intended, and resulted in increases in predator harvest, the consequences of which were not well understood because of inadequacy of population monitoring. This example appeared to support the conclusions of Robinson et al. (2008), which showed reduced age structures and high immigration rates to areas of intensive mountain lion harvest. Population declines of mountain lions further north in Idaho was considered a response to declining prey populations and increases in harvest (White et al. 2010).

WOLF HARVESTS IN CANADA AND ALASKA

Insight into wolf harvests in Canada was provided by the recorded harvest of wolves as fur (Statistics Canada 2008) and in Alaska by recorded harvests (sealed harvest) reported to ADFG. In Alaska, wolf harvest required reporting either when trapped or shot (Table 7). Wolf harvests in Alaska increased from 1984 to 2004 and declined from 2005 to 2007. The minimum number of wolves harvested, 669, was recorded in 1985, with the maximum of 1,829 in 2000. An average of 1,278 wolves was harvested each year from 1984 to 2007. These data do not include 150 to 250 wolves harvested in efforts to reduce population levels.

Trappers in Canada were also required to have their harvest recorded. The harvest fluctu-

Table 7. Wolf harvest in Alaska and Canada (Alberta, British Columbia, Manitoba, Northwest Territories, Ontario, Saskatchewan, Yukon Territories) from 1980-2006.

YEAR	AK	AB	BC	MB	NT	ON	QC	SK	YT
1980		481	228	422	486	342	3,458		92
1981		462	194	434	443	746	2,795	260	83
1982		611	184	424	523	1311	3,701	288	168
1983		494	186	379	694	1154	436	289	198
1984	1054	381	232	283	741	962	549	239	236
1985	669	456	156	293	852	1003	509	323	161
1986	806	420	201	291	732	821	592	291	102
1987	1101	370	126	252	774	647	491	213	70
1988	859	296	79	193	771	806	342	211	90
1989	940	268	79	181	734	506	389	179	78
1990	1095	246	42	177	917	391	423	220	69
1991	1208	332	64	244	1022	508	521	221	139
1992	1114	452	172	264	1207	569	592	227	180
1993	1600	399	79	445	1127	647	484	247	104
1994	1483	374	147	278	813	798	682	188	158
1995	1298	272	127	238	727	684	496	249	104
1996	1442	172	87	252	652	468	513	280	138
1997	1224	262	173	296	840	548	441	251	111
1998	1496	146	100	254	410	492	293	203	103
1999	1718	140	154	225	662	560	464	232	149
2000	1829	170	142	178	70	602	365	395	124
2001	1812	246	160	272	143	446	357	387	141
2002	1380	287	167	364	161	489	483		187
2003	1550	291	127	281	89	643	461	275	205
2004	1556	339	146	330	165	402	448	243	141
2005	1335	367	183	256	126	457	465	148	164
2006	1110	255	155	315	178	474	728	244	145
MEAN	1290	327	141	285	599	659	693	252	136

ated from 1980 to 2006 with a decrease from 1981 to 1989, an increase until 1992, and a declining trend through 2006 (Figure 5). The mean harvest over the period was 2,986 pelts with a high of 7,042 in 1982 and a low of 1,898 in 1990. The recorded fur harvest in the provinces was not considered reflective of the population trend, as trapping effort changed with pelt values and some wolves harvested were not sold for fur. Individual trappers have different objectives for trapping, with some trapping to reach a monetary goal, suggesting that the number of pelts harvested will vary with price.

In Ontario, voluntary mail surveys of hunters suggest that 1,000 to 1,600 additional

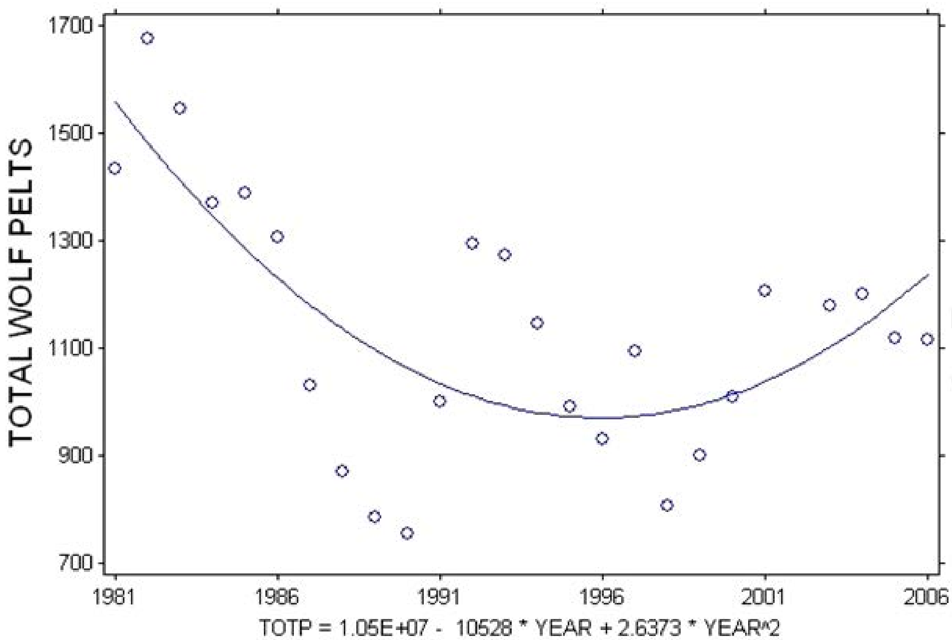

Figure 5. Total wolf pelts recorded in 8 Canadian provinces (Alberta, British Columbia, Manitoba, Ontario, Quebec, Saskatchewan, Northwest and Yukon Territories), 1980-2006 (Statistics Canada, 2007. Fur Statistics).

wolves/coyotes may be harvested annually by large and small game hunters (Ontario Ministry of Natural Resources 2004). The accuracy of these surveys was considered poor because of the difficulty of hunters visually distinguishing wolves from coyotes in the field, low survey response rates, and possible duplication of harvest data submitted by the same hunter through different surveys.

Predator control occurred in deer wintering yards from the mid-1970s to the mid-1980s in Ontario, with the objective of reducing mortality of deer in the winter when they were most vulnerable to predators. This assisted in rebuilding the province's deer populations, along with improvement of habitat, reducing hunter harvest, limiting the harvest of antlerless deer, increasing enforcement to curb poaching, and emergency feeding during severe winters. Predator control for the purpose of wildlife management has not been conducted in Ontario since the mid-1980s.

Hayes (2010) provided a record of the history of wolves in the Yukon that reflects the Canadian record reasonably well. Trappers were licensed to use poison, primarily strychnine, in 1920, which was banned in 1931 (although the practice continued illegally). The bounty on wolves was established in 1929, repealed in 1933, reinstated in 1946, and repealed in 1953. A poison campaign was initiated in 1952 and continued until 1958. Aerial wolf control was initiated in 1982 to benefit moose in the Coastal Mountains and caribou in the Finlayson region. The Aishikik wolf control experiment was established in 1992, which involved extensive aerial gunning of wolves (Hayes et al. 2003). Hayes (2010) concluded that while moose and caribou populations could be increased if wolf control was practiced effectively, the costs, adverse publicity, inability to sustain the control over time, and opportunities to use other means of managing wolf populations (including sterilization of breeding individuals) all weigh in to make traditional methods of reducing wolves questionable in the Yukon.

Gunson (1992) reported that wolf harvest reflected market demand and price before 1972 in Alberta and likely was responsible for recent declines in numbers of pelts sold on the Alberta market. However, wolf harvest by registered trappers accounted for 68% of the total harvest and was sustained, suggesting that trapping provided supplemental income for many participants. Wolf pelt values varied from a low of 76.79 CAD to a high of 150.09 (average of 106.42 CAD) from 1981 to 2006. The information provided no evidence that harvest trends in Canada were related to changes in population levels. Wolf harvest trends in Alberta were generally down over the 26 years of record, while no trends over that period were noted for the other provinces and territories. Records for individual provinces may reflect harvest from other jurisdictions since pelts may not be taken in the province where they are recorded (Gunson 1992).

Deer and moose numbers increased in many areas of Ontario in the 1990s and early 2000s (Ontario Ministry of Natural Resources 2004). While harvest trends over the last 5 years were stable, wolf numbers in most areas were either stable or increasing since 1993. More recently, mild winters resulted in increased white-tail deer numbers that subsequently resulted in increases in wolves (Rodgers, 2011, personal communication). The parasite *Parelahostrongylus tenuis* was also prevalent in areas where moose declined. The 2010 to 2011 winter of above-average snow depths has resulted in reports of deer declines, as well as declines in wolves in many parts of Ontario. Ontario's moose population is approximately 114,000 with declines in some areas and stable or upward trends in moose numbers since 1980, when the provincial population estimate was 80,000 animals (Ontario Ministry of Natural Resources 2004). The Ontario moose harvest declined from 1980 to 2008.

Records of wolf pelts sold in Quebec go back to 1917 (Figure 6). There was no trend in prices of pelts when scaled to 2008 levels. The harvest fluctuated with no apparent trend between 1917 and 1970. Pelts sold increased after 1970 (records of coyote pelts sold were included from 1970 to 1982) but have fluctuated since.

Occasional high harvests of wolves were attributable to increased availability to humans. An example of this was reported by Cluff et al. (2010) for the Border A license wolf hunt in the Rennie Lake region of the southern Northwest Territories (NT), where 3 caribou populations congregated during the 1997 to 1998 winter. Between 5 and 12 aboriginal hunters killed approximately 633 wolves. This resulted in earnings of more than 70,000 CAD for one hunter.

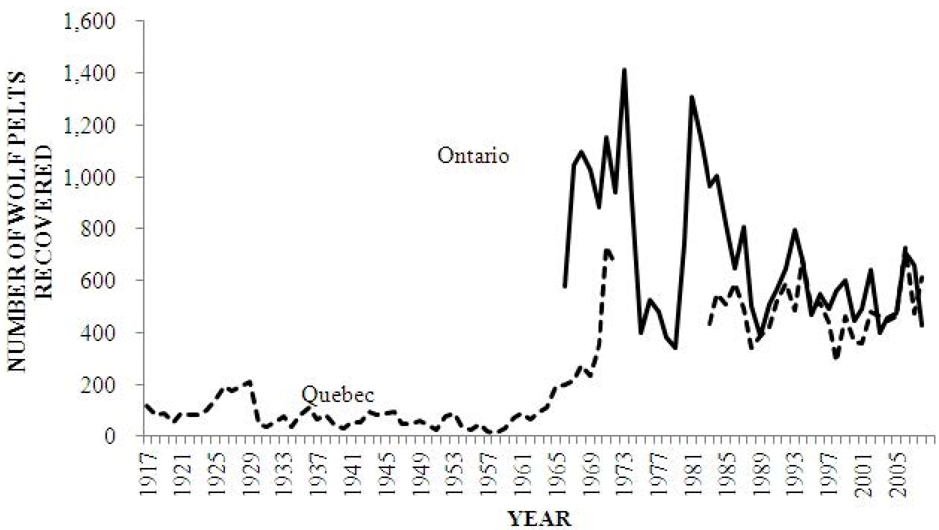

Figure 6. Ontario and Quebec wolf pelt records, 1917-2005. The Quebec information for 1973-1981 is excluded.

Cluff et al. (2010) concluded that there was wide variability in the annual wolf kill in this area, but over one-third of the tundra/taiga wolves in the NT and Nunavut may be killed in a given year, exceeding the annual threshold of sustainability. While this can influence dispersal patterns, pack structure, genetic diversity, and metapopulation dynamics, the highly variable nature of harvest from one year to the next suggested that occasional high harvests were not of long-term conservation concern. Two wolf ecotypes, boreal resident and tundra/taiga migratory, were involved, which complicated monitoring and influences of harvest.

The records from Alaska and Canada likely track harvest trends but do not represent total harvests. Some furs were used locally in clothing and crafts and were not reported. Hunter harvest is also not included in the records. As such, the recorded harvest by registered trappers and of harvest as fur may not represent the trend for total harvest (Robichaud and Boyce 2010). Changing values due to inflation affect the relationship between harvest and value. Costs of fuel and other equipment also must be considered. Average value of wolf hides in Alaska may be higher than average price paid at auctions. Average value of fur recorded in western Canada was 120,957.00 CAD per year over the 26-year period. Highest values come from the northern wolf ranges, suggesting that natives and others living in those areas were the primary trappers and hunters, and this probably applied to Alaska. Mean prices per pelt changed from a calculated average of 83.75 CAD in 1981 to 133.15 in 2006, approximately a 59% increase. However, the Consumer Price Index in Canada changed from 49.5% of the 2002 index to 114.1% of the index in 2008, a 97.7% increase overall (Statistics Canada 2009). Considering fuel prices and other costs, wolf trapping has not been an exceptionally lucrative endeavor over the past 27 years.

Wolf populations can sustain hunting mortality of 30% of the winter population (Fuller 1989). Immigration of wolves from adjacent populations is an important influence on the rate of recovery. Regelin's (2002) conclusions that localized, continuous management of wolf populations involving agency personnel and citizens would be necessary were supported by these observations.

Moose harvest trends in Canada are more influenced by numbers of hunters and changes in habitat than predation (Table 8). Harvests in British Columbia, Manitoba, Ontario, and the Yukon Territory declined from 1980 to 2009, while harvests in the eastern provinces of New Brunswick, Newfoundland, and Nova Scotia have increased. These records are for the total provincial harvest in each case, and obscure local situations where predation may be an important factor. An example of where wolf predation is considered to reduce moose, elk, caribou, and stone sheep (*Ovis dalli stonei*) populations occurs in northeastern British Columbia. A combination of outfitters, hunters, and others coordinated efforts to reduce wolf populations without including the provincial wildlife agency. The effort is in line with recommendations of Regelin (2002) to encourage localized management by residents as a more practical means of managing wolves, although the wildlife agency should obviously be involved.

WOLVES IN THE ROCKY MOUNTAIN REGION

The gray wolf introductions of 1995 and 1996 into the northern Rocky Mountain states produced an estimated total of 1,687 wolves and 113 breeding pairs by 2009 (U.S. Fish and Wildlife Service et al. 2010). Accuracy of the estimates can be questioned, but the reintroduction resulted in establishment of viable populations of wolves that were well-distributed across the recovery areas. A total of 1,258 wolves were killed and another 117 have been moved since 1995 to reduce depredations on livestock and dogs. A total of 1,301 cattle, 2,154 sheep, and 142 dogs were killed by wolves from 1987 to 2009. Idaho and Montana held wolf seasons in 2009, with quotas established for 200 in Idaho and 75 in Montana. As of March 2010, 188 wolves were harvested in Idaho and 72 in Montana.

Table 8. Moose harvest in Alaska and 7 Canadian Provinces (British Columbia, Manitoba, Ontario, New Brunswick, Newfoundland, Nova Scotia, Yukon Territories), 1980-2009. Trends are up for AK, NB, NL, and NS and down for BC, MB, ON, and YT over the period.

YEAR	AK[1]	BC[2]	MB	ON	NB	NL	NS	YT[3]
1980		12,486	2,074		1,230	8,230		1,007
1981	5,613	12,046	1,675		1,436	7,617		971
1982	5,086	12,792	1,583		1,344	7,056		1,072
1983	7,230	10,750	1,668		1,287	7,531		829
1984	7,716	10,364	1,786	10,359	1,618	8,536		869
1985	6,424	11,573	1,472	10,436	1,346	9,579		811
1986	7,619	13,489	1,749	11,224	1,625	10,429	185	765
1987	7,174	13,463	1,411	10,399	1,838	10,993	164	767
1988	7,685	13,539	1,454	11,287	1,473	12,340	183	845
1989	7,257	13,637	1,236	10,272	2,022	14,677	168	789
1990	5,999	13,457	1,209	11,137	1,657	18,305	130	824
1991	7,017	12,251	1,028	11,313	1,753	20,663	113	847
1992	6,237	11,557	1,144	10,170	1,899	19,648	131	680
1993	7,290	10,025	1,350	10,523	2,061	18,956	161	777
1994	7,089	9,944	1,475	11,380	2,094	20,784	177	680
1995	7,036	11,047	1,510	10,924	2,326	17,684	175	837
1996	8,689	9,701	1,186	9,739	1,715	19,020	175	752
1997	8,354	10,494	949	9,924	2,121	20,009	181	800
1998	8,391	11,438	1,114	10,535	2,427	19,943	188	850
1999	7,525	7,459	1,106	9,586	2,022	19,112	182	712
2000	7,034	9,182	1,229	9,801	2,537	18,303	190	747
2001	6,652	10,290	1,170	11,409	2,573	17,918	186	763
2002	7,040	10,803	863	9,069	2,071	18,188	189	700
2003	6,984	11,309	1,260	9,684	1,568	18,677	262	650
2004	6,925	9,571	783	8,317	1,794	16,837	290	676
2005	7,416	9,980	1,101	8,955	2,084	17,544	279	722
2006	7,360	9,939	1,125	8,066	2,362	19,063	305	720
2007	7,737		1,019	7,291	2,120	18,699	264	673
2008	7,930		1182[&]	6,263	2,231	18,915	274	776
2009	8,206		827[&]	6,057	2,409	18,498	300	655

[1]Ak has no mandatory check and harvest in remote villages is known to be underestimated and unreported. This applies to the Canadian data as well.
[2]Resident and nonresident totals
[3]Does not include kills by First Nation members.
Starting in 2001, resident hunters had to report their moose kills on a Yukon Biological Submission/Kill Report form. Prior to 2001, resident hunters reported their moose kills through a mail questionnaire. Hunters report their moose kills through an outfitter hunter declaration form.
Prior to 2001, resident harvest reported by mail questionnaire. Nonresident harvest reported through an outfitter declaration form.

Most wolves were opportunistically harvested by hunters who were primarily hunting elk or deer. The harvest removed approximately 5% of the Montana population and 12% of the Idaho population. Agency control (145 wolves) and hunting removed 28% of the estimated wolf population in Montana, while control of 134 wolves plus hunter harvest removed 20% of the minimum population in Idaho. Agency control removed 32 wolves or an estimated 9% of the Wyoming population, which was not hunted. Documented pack activity was reported in 2009 in Oregon and Washington. Litigation resulted in placing wolves in Montana and Idaho back on the Endangered Species list in August 2010, but the U.S. Congress passed legislation removing the wolf from the list in March 2011 in Montana and Idaho. The wolf is still listed in Wyoming.

Estimates of wolves inhabiting Yellowstone National Park suggest that at least 124 wolves including 12 packs were present in 2008. This represented a decline of 27% from the 2007 estimate, and a 30% decline from 2005. Six of 12 packs produced pups, which was the lowest number since 2000 (U.S. National Park Service 2012). Elk, the major prey species, occupying the northern range declined from over 17,000 prior to wolf reintroduction in 1995 to over 6,000 in winter 2008. Additionally, elk distributions have changed to where 3,000 to 4,000 animals winter in the park, with the rest moving north to winter at lower elevations outside of the park. The decline in elk was largely attributable to continuing effects of predation by wolves and brown bears, according to the Northern Yellowstone Wildlife Working Group, with 2 severe winters. Numbers of elk wintering inside the park appear to have leveled off since 2006 (U.S. National Park Service website 2010).

Areas in the Greater Yellowstone Ecosystem, a 56,000-km^2 area that includes Yellowstone National Park, several national forests, and private lands, were essentially fully occupied by wolves, with between 31 and 38 breeding pairs and 390 to 455 wolves in the fall population since 2006 (U.S. Fish and Wildlife Service et al. 2010). Elk that wintered in the interior portions of the park have been substantially reduced, while elk wintering 40 km north of the park in the broad valley of the Madison River drainage have increased in recent years (Hamlin et al. 2009). Wolves were controlled primarily to reduce depredations on livestock outside of the park. The experience thus far has suggested that the added presence of wolves in the region has caused elk to decline in traditional wintering areas where wolves were not managed, while elk populations have either been maintained or increased where wolves were managed.

WOLVES IN THE WESTERN GREAT LAKES REGION

At least 3,949 wolves inhabit the western Great Lakes states in Michigan (520), Minnesota (2,922), and Wisconsin (549) (U.S. Fish and Wildlife Service 2009). These wolves were listed as threatened in Minnesota and endangered in Wisconsin and Michigan, and were not subject to hunting. The Isle Royale wolf population fluctuated from over 50 in 1979 to 12 animals in the late 1980s to early 1990s, and was approximately 16 in winter 2011 (Vucetich and Peterson 2011).

Mech (2001) reported on management of wolves in Minnesota if they were to be delisted and management turned over to the state. Complete protection for wolves, except for those causing depredations, should continue for 5 years after delisting. Approximately 83% of the wolves were located in the northeastern third of Minnesota, where restrictions on harvest were more rigorous than in the rest of the state. The 1998 estimate was 2,450 wolves, but no trends in wolf numbers or distributions were thought to exist from 1998 to 2008. The federal recovery team recommended a population goal of between 1,250 and 1,400 wolves for Minnesota, with none in the agricultural regions. Mech (2001) estimated that at least 110 wolves would have to be harvested to limit wolf range expansion, and between 929 and 1,956 to reduce the population below levels related to natural mortality and depredation control. The most effective management approaches seemed to focus on harvesting wolves out of agricultural areas, where most depredations were occurring. In areas where predation on deer and moose was deemed excessive, Mech (2001) concluded that a sustained effort involving both federal and state agents would have to occur.

Efforts to maximize public acceptance of wolf harvesting will be difficult (Mech 2010). Efforts to reduce public opposition include opening season after most pups reach adult size, usually in November, so as to reduce killing pups. This timing also enhances pelt preservation, helps ensure that pelts are prime, and reduces harvest

PHOTO CREDIT: Government of Newfoundland and Labrador

This Newfoundland black bear was tagged by scientists in the Department of Environment and Conservation as part of a study analyzing caribou calf mortality.

of wolves frequenting rendezvous sites. Ending seasons in early March would also coincide with loss of prime pelt condition. Regulations should attempt to focus wolf harvests in areas where conflicts between wolves and ranching operations occur. Mech (2010) also recommended efforts to concentrate public takings in areas where increases of their prey were desired. States need to be able to adapt management as conditions change and experience increases. Consideration of wolf biology and public sensitivities in wolf harvest regulations could help maximize recreational value of harvests, minimize public animosity, and accomplish population management objectives (Mech 2010).

MEXICAN GRAY WOLVES

Only 50 Mexican gray wolves were estimated to exist in the Blue Range recovery area in Arizona and New Mexico as of 2010 (U.S. Fish and Wildlife Service 2010). Ninety-two wolves were released into this recovery area between 1998 and 2009, with 71% (65) released between 1998 and 2001. Illegal shooting had accounted for 31 of 70 known mortalities, with vehicle collisions accounting for 12 deaths. The number of known breeding pairs dropped from a high of 7 in 2006 to 2 in 2010. The population was approximately half of the 102 wolves that a 1996 environmental impact statement (EIS) projected would occur by 2006, illustrating the difficulty of establishing populations in this recovery area.

BEAR HARVEST AND POPULATION MANAGEMENT

Black Bears

Black bears are the most abundant large carnivore (>30 kg) in North America and perhaps the world. They are managed primarily as game animals depending upon the demographics, geography, and local traditions of jurisdictions. Hunting regulations largely depend on hunter numbers, access, effectiveness, public safety, and local culture, concurrent with species population productivity (Hristienko and McDonald 2007).

A problem common to all jurisdictions is obtaining adequate information on bear populations to judge effects of management (Miller et al. 1997, Garshelis and Hristienko 2006). Garshelis and Hristienko (2006) concluded that population estimates were a poor index of population size but can be useful in managing bear harvest. The validity of population estimates at the provincial and state level was questionable because of the lack of sufficient data. Nearly half of the agencies surveyed reported that observed trends in black bear populations were different from the population estimates they used. Some agencies indicated that they adjusted their estimates to reflect a perceived trend, and some, in hindsight, revised past estimates. Hristienko and McDonald (2007) reported that of 52 North American jurisdictions surveyed in 2002, only 9 states provided empirically-derived population estimates. Black bears are so abundant in some jurisdictions that there is no pressing need for quantitative enumeration.

Eastern Populations.— Black bear population trends in 6 provinces and 26 states in eastern North America were surveyed by Hristienko and Olver (2009). Based on mid-point estimates provided by the same jurisdictions in a 2001 survey (Hristienko & McDonald 2007), Hristienko and Olver (2009) reported that 18 jurisdictions had increasing populations: New Brunswick, Newfoundland, and Quebec in Canada, and the states of Connecticut, Florida, Georgia, Louisiana, Maryland, Massachusetts, Mississippi, New Jersey, New York, Ohio, Rhode Island, South Carolina, Tennessee, Vermont, Wisconsin. Four states indicated population decreases: Michigan, Minnesota, North Carolina, and West Virginia. And eight jurisdictions identified no change: Manitoba, Ontario, Alabama, Arkansas, Kentucky, Maine, New Hampshire, and Pennsylvania. Nova Scotia and Virginia chose not to provide an estimate for 2007. Eighteen (56%) of the estimates were empirically derived.

Using mid-point estimates provided in 2000 (Hristienko & McDonald 2007) and 2007 (Hristienko and Olver 2009), black bear populations in eastern parts of Canada and the U.S. increased by 6% and 4%, respectively. The authors noted that 3 U.S. jurisdictions (Michigan, Minnesota, and North Carolina) provided reduced population estimates, with Minnesota being the only jurisdiction to report a declining population trend. Ranges were expanding in 8 jurisdictions, stable in 23, and contracting in Vermont.

Black bear harvests in the eastern U.S. (from Minnesota and Arkansas eastward) increased from 1985 to 2007 (Table 9). All major bear producing states showed increased harvests, averaging 16,153 total bears (range 5,132 in 1985 to 25,700 in 2006). Initial seasons occurred in 1985 in South Carolina, 2003 in New Jersey, and 2004 in Maryland. Florida stopped hunting bears in 1993. The total harvest in eastern Canada (from Manitoba eastward) showed no trend (Figure 7), averaging 11,234 per year (ranging from 8,412 in 1999 to 14,029 in 1995). However, increased harvest in Nova Scotia, New Brunswick, and Newfoundland was obscured because about 82% of the total harvest occurred in Ontario and Quebec. Nova Scotia initiated a hunting season in 1988.

Although harvest data may be the most reliable information that agencies obtain, it is far from complete. Six states (Arkansas, Georgia, New York, North Carolina, Tennessee, and Vermont) did not offer a separate license for black bears but did allow the harvesting of a bear under the authority of a combined big game license. These jurisdictions were unable to determine how many license holders hunted bear. Of 23 eastern jurisdictions that had a black bear hunting season in 2007, only 16 (69%) had continuous or complete hunter/harvest data. For the com-

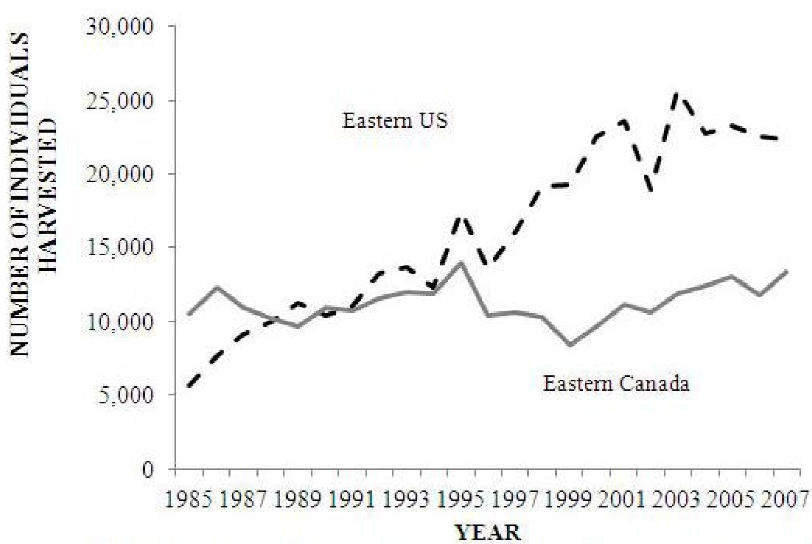

Figure 7. Black bear harvests in eastern U.S. (Minnesota-Arkansas, east) and eastern Ca
(Ontario east).

Table 9. Black bear sport harvests in western states and provinces, 1980-2008.

YEAR	AK	AZ	CA	CO	ID	MT	NM	OR	UT	WY	WA	AB	BC	MB	SK	YT
1980	1,211	255	592	461	1,619		195	958	26	159			5,670		1,377	91
1981	1,207	287	767	452	1,918		292	783	39	187			3,247		928	128
1982	1,076	260	783	521	1,584		253	1,313	38	263			3,180		1,121	89
1983	1,305	273	601	539	2,100		232	1,420	18	196			3,557		1,071	96
1984	1,562	246	770	406	2,100		250	1,350	26	205			3,531		2,050	139
1985	1,688	251	1,138	613	1,700	957	254	1,250	29	203			3,167		1,668	112
1986	1,727	182	1,040	468	2,150	1,058	230	1,376	72	248			3,348		3,109	98
1987	1,563	302	1,448	532	1,950	984	266	954	44	195			2,679		2,628	110
1988	1,577	146	1,359	631	1,900	920	290	803	69	234			3,342	1,627	2,067	132
1989	1,501	271		580	2,100	1,064	397	664	97	220		1,581	2,953	1,661	1,584	106
1990	1,720	149	1,187	402	2,300	1,113	387	888	22	228		862	2,840	201	1,689	103
1991	1,741	96	1,493	431	2,100	883	276	1,172	35	244	1,379	1,134	3,306	1,676	1,483	92
1992	1,765	121	1,266	482	2,800	1,215	229	805	32	229	1,442	699	3,480	1,587	1,586	103
1993	1,533	117	1,426	283	1,260	1,013	348	1,179	35	255	1,507		3,297	1,388	1,886	70
1994	1,763	236	1,607	362	2,250	1,033	625	1,250	42	231	1,073	716	2,850	1,496	1,564	99
1995	1,835	197	1,484	533	2,040	1,142	526	624	53	169	1,218	1,357	3,063	1,063	1,659	90
1996	1,940	254	1,714	520	1,740	1,000	407	880	68	157	1,310	1,036	3,124	1,907	2,040	103
1997	2,048	224	1,677	465	1,538	1,164	289	649	50	186	844	1,066	3,011	1,364	2,280	112
1998	2,570	142	1,676	557	1,973	1,221	148	836	46	204	1,802	967	2,829	1,519	2,362	82
1999	2,313	181	1,836	854	1,819	1,154	216	856	57	205	1,105	1,022	3,613	1,634	2,316	92
2000	2,689	320	1,796	820	1,855	1,140	340	977	75	226	1,148	1,207	2,826	1,549	2,656	113
2001	2,508	178	1,633	759	1,887	1,009	596	625	68	315	1,439	1,000	2,814	1,864	2,372	104
2002	2,534	230	1,768	858	2,390	1,168	745	950	83	365	1,725	965	2,650	1,750	2,527	60
2003	2,465	214	1,672	599	2,426	1,211	455	867	86	272	1,566	1,420	2,789	1,740	2,407	123
2004	2,475	160	1,848	507	2,443	1,508	238		105	318	1,654	1,456	1,708	1,971	626	83
2005	2,810	158	1,413	454	2,425	1,114	290	716	80	299	1,333	1,534	2,185	1,905	639	65
2006	3,145	197	1,822	451	2,231	1,043	357	989	86	287	1,642	1,345	2,005	2,088		75
2007	3,365	221	1,861	615	2,660	744	372		127	320		1,667		1,934	618	78
2008	2,776		2,028	760		1,216	333		134					2,038		76
MEAN	2,014	210	1,768	549	2,045	1,086	339	967	60	236	1,387	1,169	3,076	1,617	1,789	97
SD	609	59	165	145	351	149	138	246	31	53	264	292	692	409	671	20
LOW	1,076	101	1,413	278	1,538	933	148	624	27	261	844	699	1,708	201	618	60
HIGH	3,365	368	2,028	831	2,800	1,224	745	1,376	205	323	1,802	1,667	5,670	2,088	3,109	123

parative periods of 2000 and 2007, the number of hunters and bears harvested in eastern Canada increased by 25% and 20%, respectively; while for the same periods, hunter numbers in the U.S. increased by 13% but harvests declined by 4%. Harvest rates varied from 2.5% in South Carolina to 22.4% in Minnesota. On average, the harvest rate for eastern Canada was 7.4%, while in eastern U.S. it was about 12.3%.

All but 4 jurisdictions had bag limits of 1 bear. Newfoundland and West Virginia had bag limits of 2 bears, while Ontario and Minnesota had a bag limit of 1 bear but did allow a second bear to be harvested in some game management units. There was no spring season in any of the eastern states, although at least one Native American tribe allows spring hunts on their lands in Maine. All provinces except Ontario and Nova Scotia had a spring season in eastern Canada. The use of bait was permitted in all 6 eastern Canadian provinces, and in 7 (41%) eastern U.S. states (Arkansas, Maine, Michigan, Minnesota, New Hampshire, North Carolina, and Wisconsin). Hunting dogs could be used in Ontario, Georgia, Maine, Michigan, North Carolina, New Hampshire, South Carolina, Tennessee, Vermont, Virginia, West Virginia and Wisconsin.

Western Populations.— Black bear harvests in the western tier of the continent likely reflected combinations of population size, hunting conditions, characteristics of hunting seasons, changes in habitat conditions that affect distribution, and hunter interest. Harvest information from 10 western states and 4 provinces provided additional insight (Table 10). The highest harvest of black bears in the western part of the continent outside of Alaska from 1980 to 2007 occurred in British Columbia (averaging >3,000 bears per year) and in Idaho (averaging >2,000 bears per year). The lowest mean harvest over that period was in Utah, which had the least amount of suitable habitat. The 3 west coast states had high harvest numbers, likely a reflection of high-quality habitat. There was no black bear hunting in Nevada.

Enough information was available for Arizona, British Columbia, Colorado, Idaho, New Mexico, Oregon, Utah, and Wyoming to examine harvest trends over the 27-year period. There was no apparent trend in harvest for Arizona and Colorado, but a significant increase in harvest levels occurred for the other states, and a decline in harvest occurred in British Columbia (Figure 8).

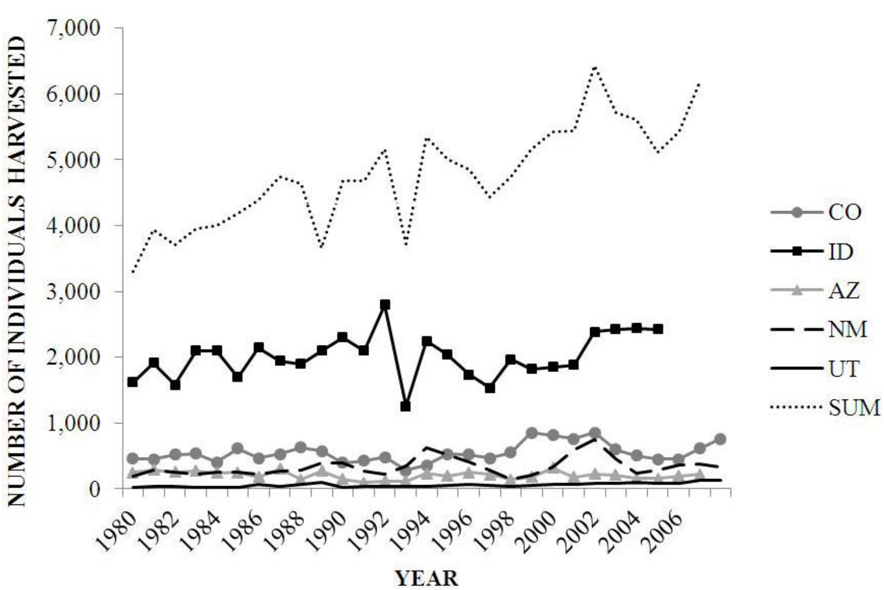

Figure 8. Black bear harvests in 5 western states (AZ, CO, ID, NM, UT), 1980-2008.

Table 10. Black bear sport harvests in eastern states and provinces, 1985-2007.

YEAR	AR	FL	GA	MA	MD	ME	MI	MN	NC	NH	NJ	NY
1985	23	68	46	14	*ns	1,544		1,340	323	93	*ns	422
1986	13	51	57	18	*ns	1,955		1,438	409	126	*ns	747
1987	7	45	61	34	*ns	2,394		1,577	553	260	*ns	626
1988	14	41	100	37	*ns	2,652		1,509	567	198	*ns	755
1989	30	60	96	29	*ns	2,690		1,911	547	241	*ns	880
1990	19	40	114	29	*ns	2,088	739	2,350	759	291	*ns	660
1991	102	60	99	25	*ns	1,665	1,084	2,143	716	123	*ns	763
1992	44	22	100	68	*ns	2,042	1,225	3,175	1,059	230	*ns	827
1993	115	64	217	59	*ns	2,055	1,292	3,003	821	274	*ns	695
1994	126		141	62	*ns	2,243	1,260	2,329	785	239	*ns	722
1995	133		208	134	*ns	2,645	1,522	4,956	1,084	428	*ns	693
1996	207		132	56	*ns	2,246	1,266	1,874	1,010	152	*ns	642
1997	187		206	78	*ns	2,300	1,315	3,212	1,463	335	*ns	525
1998	170		254	59	*ns	2,618	1,545	4,110	1,300	279	*ns	597
1999	202		273	98	*ns	3,483	1,817	3,620	1,366	499	*ns	685
2000	181		300	81	*ns	3,951	2,011	3,898	1,490	449	*ns	1,070
2001	372		279	104	*ns	3,903	2,268	4,936	1,533	527	*ns	800
2002	263		262	116	*ns	3,512	2,282	1,915	1,485	338	*ns	912
2003	309		333	153	*ns	3,900	2,465	3,598	1,812	803	328	1,864
2004	340		212	146	20	3,921	2,221	3,391	1,497	679	*ns	1,014
2005	345		365	113	40	2,873	2,210	3,340	1,661	434	298	1,066
2006	332		303	148	41	2,659	2,639	3,290	1,800	352	*ns	796
2007	400		425	143	51	2,871	2,181	3,172	2,005	614	*ns	1,117
MEAN	171	50	199	78	38	2,705	1,741	2,873	1,132	346	313	821

Table 10 cont. Black bear sport harvests in eastern states and provinces, 1985-2007.

YEAR	PA	SC	TN	VA	VT	WI	WV	NB	NL	NS	ON	PQ
1985	1,029	1	45	402	168		114	631	443		7,814	1,626
1986	1,362	2	54	505	246	503	132	771	336		8,701	2,455
1987	1,560	6	64	564	305	837	251	924	529		7,470	1,964
1988	1,614	4	76	573	368	1,125	388	993	496	52	6,340	2,330
1989	2,220	10	78	629	311	978	514	980	346	36	5,668	2,689
1990	1,200	2	123	330	163	1,247	235	1,054	446	99	6,531	2,815
1991	1,687	5	63	655	237	1,219	428	780	486	178	6,763	2,484
1992	1,589	9	74	486	338	1,474	455	1,007	607	76	6,892	3,000
1993	1,760	2	100	781	363	1,258	767	1,153	636	111	6,771	3,311
1994	1,365	8	120	521	336	1,328	737	1,311		248	7,201	3,137
1995	2,190	12	81	607	382	1,737	694	1,384	515	286	8,143	3,701
1996	1,796	14	121	620	288	2,325	772	1,369	515	247	5,868	2,378
1997	2,110	20	366	789	287	2,178	691	1,300	350	191	6,527	2,238
1998	2,598	14	108	898	324	3,184	1,090	1,330	497	243	6,348	1,899
1999	1,741	19	171	920	472	2,881	997	1,434		208	4,124	2,646
2000	3,075	42	117	1,003	432	3,075	1,316	1,929		264	4,468	3,043
2001	3,063	21	159	880	524	2,986	1,257	1,781	355	226	5,486	3,307
2002	2,686	27	150	931	297	2,471	1,357	1,905	422	284	4,842	3,218
2003	3,004	55	234	1,516	722	2,905	1,699	1,956	530	393	5,417	3,577
2004	2,974	29	167	1,130	730	3,063	1,235	2,111	437	741	5,254	3,874
2005	4,162	34	308	1,352	442	2,645	1,634	1,978	558	573	6,110	3,867
2006	3,124	51	309	1,644	324	3,068	1,704	1,924		932	5,371	3,512
2007	2,360	58	337	1,523	425	2,797	1,804	1,864	591	650	6,204	4,005
MEAN	2,186	19	149	837	369	2,058	881	1,386	479	302	6,274	2,916

Black bear seasons in back country areas of Idaho were liberalized in 2000 in response to sportsmen's concerns of black bear predation on elk calves, with 2 tags permissible per hunter and a reduced tag cost for nonresident hunters (Nadeau 2007b). Harvest data for the roadless portions of the Salmon River region show that 3-year-old male bears were most frequently harvested. The annual harvest in this region averaged 37.5 bears from 1994 to 1999 and 53 bears from 2000 to 2006, an increase of 41%. Harvests were considered to be within acceptable limits during the entire 13-year period.

Bear complaints and conflicts resulting in handling bears increased from 1997 to 2008 in western Nevada (Nevada Division of Wildlife 2009). The policies used in Nevada were representative of other states. Traps to capture offending bears were not set unless attractants were removed or exclusionary precautions taken. The Nevada Division of Wildlife (NDOW) handled 5 bears in 1997 and a high of 157 in 2007, with a total of 654 bears handled over the 12-year period.

Wildlife agencies monitor the proportion of females in the harvest as a means of determining population effects. The proportion of females in the harvest is not considered to affect population levels when it is around a third of the total harvest. New Mexico changed from statewide seasons to a zone system in 2004. Prior to the change, an average of 343 bears (range 148-745) were harvested annually with 37.3% (range 28.5-43.7%) being females. After the change to the zone system, an average of 318 bears (range 238-372) were harvested, with 33.1% (range 28.2-38.6%) being female. Percent hunter success changed from an average of 6.8% (range 4.2-12.7%) to 6.48% (range 4.4-8.0%). The number of hunters averaged 4,382 per year prior to the change to 4,967 hunters per year afterwards. The zone system reduced the average number of bears harvested, reduced the number of females in the harvest, and caused a minimal decline in hunter success, but the number of hunters increased.

Washington managed black bears to keep the proportion of females in the harvest at 35-39%, the median age of harvested females at 5-6 years, and median age of males at 2-4 years (Washington Department of Fish and Wildlife [WDFW] 2008). If the median age declined and the proportion of females increased beyond those levels, then reductions in harvest were indicated. These criteria were recognized as weak indicators of population status, but they were obtainable at acceptable cost and effort.

Human-Bear Conflicts

Safeguarding human welfare and minimizing damage to crops, livestock, and property becomes a delicate balance as human populations expand into areas occupied by bears and as bears reoccupy unmanaged land that was once cultivated. Concurrent with the expansion in numbers and distribution of both bears and people, human-bear conflicts have been increasing. These typically involve crop and livestock depredation, vehicular collisions, and residential property damage. In addition to increases in property damage, threats to human safety have also increased. This decade alone, there were 17 black bear inflicted fatalities, as well as an average of 15 non-fatal attacks a year (Herrero et al. 2011). These fatalities represent 27% of the 63 recorded since 1900.

Public attitudes turn against bears as damage to property, crops, and livestock increases and bear numbers are not managed. It then becomes necessary to remove individual bears that are threatening people or have become habituated and/or food-conditioned. To prevent the latter, residents and visitors of bear-occupied land need to be vigilant in eliminating or securing all potential food sources. Education and enforcement of regulations are keys to preventing bears from establishing home ranges in human-occupied lands. Formal "Bear Aware" programs to educate the public as well as remove attractants are ongoing across much of British Columbia. However, Baruch-Mordo et al. (2011) did not find education to be particularly effective in Colorado and recommended application of proactive enforcement such as warning notices to reduce bear depredations.

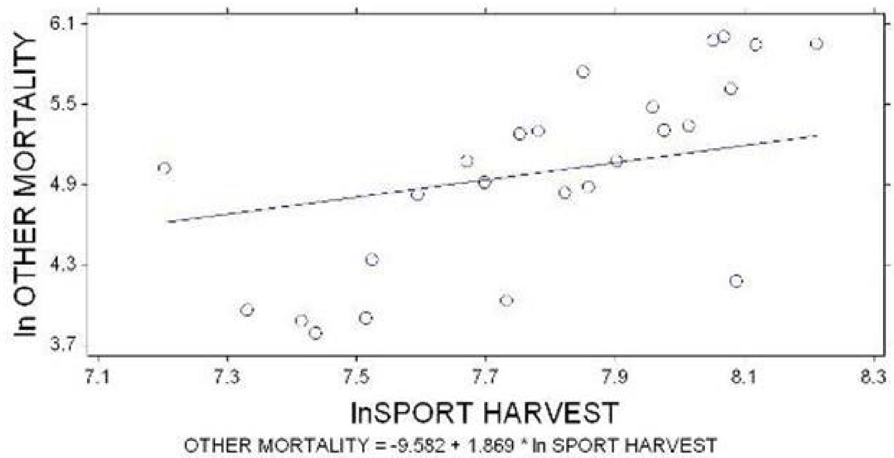

Figure 9. Black bear sport harvest compared with other causes of mortality in 5 western state (AZ, CA, CO, NM, UT).

Damage to private property by bears often results in the offending animals being killed. Hristienko and Olver (2009) reported an average of 652 bears being disposed of between 2003 and 2007 across a predominantly rural landscape in eastern Canada, while throughout the urban U.S. only 307 were killed because of conflict. Human-bear conflicts across eastern provinces ranged from 9,002 to 18,214 over the same period. These figures were similar across the eastern states, 9,767 to 18,270, despite differences in both human and bear population numbers. However, the urban U.S. recorded 5 times as many bears killed by vehicles than Canada, 1,327 and 272, respectively.

A comparison of sport harvest and depredation mortality for the west and southwest shows that as sport harvest increased, so did other kinds of human-caused mortality (Figure 9). Annual variation in natural foods was related to depredations, but the information suggested that as population levels increased and bears came into contact with human habitations more frequently, depredations also increased. This suggested that harvest should not be expected to reduce other forms of human-caused mortality on a broad scale, especially when hunter harvest was closely regulated. Treves (2009) concluded that evidence that hunting prevents property damage or reduces competition for game is weak. Hunters appear not to be hunting bears that are most likely to cause property damage. However, the correlation between depredations and harvest levels suggested that general reductions in bears through hunting, particularly in areas where damages were apt to occur, could assist in reducing depredations.

Instances of black bears killing and eating humans have been recorded for years, with the latest individual being a woman who purposefully fed bears in southwestern Colorado (Bunch 2009). Wildlife officials in Conklin, Alberta killed 12 black bears that were scavenging at a landfill and had been fed by people as well (Alberta Wilderness Association 2009). No matter how much publicity and cautions are provided to the public, there will always be individuals who choose to ignore them and then suffer the consequences, along with the bears.

Brown Bears

Brown bears are considered extirpated in the prairies of Alberta, Saskatchewan, and Manitoba (COSEWIC 2002), are listed in the subjective category “species of concern” in Canada by COSEWIC, and are a hunted species in the Yukon, Northwest Territories, Nunavut, and British Columbia. In the contiguous U.S., they are listed as threatened (U.S. Fish and Wildlife Service 2009). Alaskan brown bears are man-

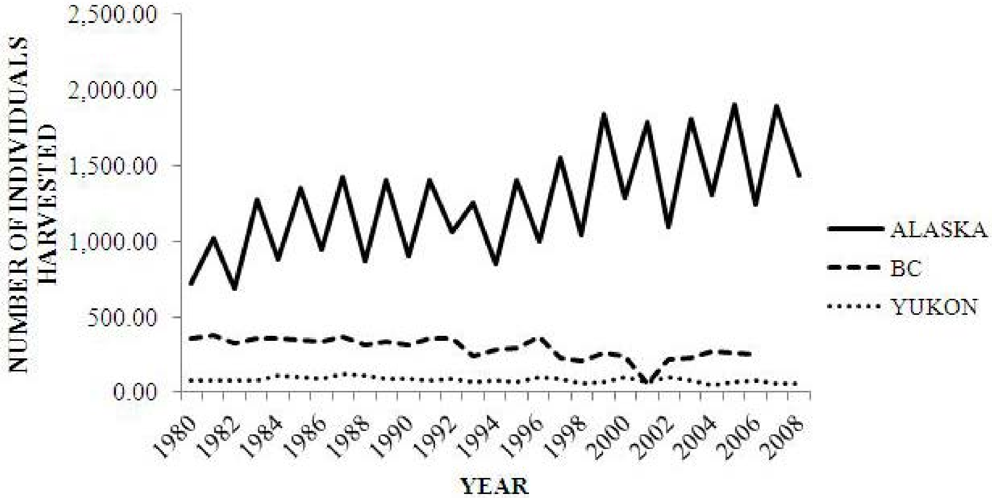

Figure 10. Brown bear harvests in Alaska, British Columbia, and the Yukon Territory, 1980-2006.

aged as a hunted species, with current efforts to reduce the interior brown bear population being a major management objective.

Brown bear harvests by residents in British Columbia (BC) declined slightly from 1980 to 2008 (Figure 10), coinciding with a decrease in other human-caused mortality. The brown bear harvest in the Yukon fluctuated with no evident trend from 1980 to 2008. Non-hunting mortality was highly correlated with a decline in other types of human-caused mortality in BC, but not in the Yukon. Programs to reduce non-hunting mortality with "Bear Aware" programs to reduce attractants and install electric fences around garbage dumps have helped to reduce non-hunting mortality. An increasingly conservative harvest coupled with increased public controversy over non-resident harvests in B C contributed to the declining harvest trend in the province. The correlation between harvest levels and brown bear populations in BCand the Yukon was unknown but likely not high.

Brown bears in Alberta are considered a species of special concern and a moratorium on hunting was initiated in 2006. Population estimates using DNA-based mark-recapture studies in a major portion of the occupied habitat provided an estimate of 582 bears from Grande Prairie to the southern border, and expanded to an estimate of 691 for the province (Alberta Sustainable Resource Development and Alberta Conservation Association 2010). Management plans aim to increase the population to 1,000 (Alberta Fish and Wildlife Division 1990). Road expansion has lead to high mortality rates. Known mortality between 1972 and 1996 was partitioned between legal hunting (65%), illegal activities and self-defense (13%), aboriginal harvest (4%), problem bear removals (9%), and other sources including vehicle accidents (9%). Legal harvest and removals by authorities were considered accurate, but mortality estimates from other causes of mortality were less reliable.

Brown bear harvests increased in Alaska and reflected increased population in coastal areas and efforts to reduce populations of interior bears between 1980 and 2008. An average of 1,265 bears was harvested from 1980 to 2008, with a low of 723 in 1980 and a high of 1,906 in 2005. Climate change and increased salmon escapements may have resulted in increased productivity and size of coastal bear populations. Increases in harvests of interior brown bears were attributable to liberalized regulations purposefully intended to reduce population levels to minimize predation on moose and caribou. The zigzag pattern of the Alaska bear harvest is attributable to seasons that are open every other year on the Alaska

Peninsula, where a large portion of the total harvest is harvested.

The highly regulated Kodiak brown bear harvest showed no significant trend from 1980 to 2008, but increased from about 150 bears in 1980 to 170 in 2008. The population on the Kodiak Archipelago was considered to be slightly increasing and was estimated at approximately 3,500 bears in recent years (Van Daele 2008). Evidence of conservative harvests was the increase in the harvest of large males from 2.5% in 1970s to 9% in the 1990 to 2000s. Non-sport harvest ranged from a low of 6.1% of the estimated population in the 1970s to a high of 23.7% in the 2000s, generally coinciding with population increases (ADFG records on file, Kodiak, Alaska).

Miller et al. (1998) examined attitudes of Alaskan voters, resident hunters, and nonresident hunters toward black bears and Alaskan brown bears. They reported that in general, Alaskans were interested in and tolerant of wildlife. Almost half of the voters and resident hunters liked having the bears in urban environments, the majority of respondents opposed baiting, and though most voters supported hunting for meat, they were less supportive of hunting for trophies. Miller et al. (1998) concluded that although Alaskans liked wildlife viewing areas, they were not willing to sacrifice any hunting opportunities for them. They also reported that bear viewing opportunities were in high demand, and residents were willing to pay an average of $759 to see bears.

Human-brown bear interactions are common in Alaska. Managers have collected some information on the nature of these interactions to facilitate reductions in incidents as outdoor recreation becomes increasingly popular, especially in the parks. Barnes (1994) reported that among deer hunters surveyed on Kodiak Island, half observed a brown bear during the hunt and 21% reported a threatening encounter with a bear, with some losing deer meat to bears. Albert and Bowyer (1991) reported that brown bear incidents were reduced by 92% after a bear-human conflict management plan was initiated in Denali National Park, which improved garbage disposal, required bear-resistant containers for campers, and implemented an information program. They reported that interactions were more prevalent in the backcountry areas of the park, with almost half of the reports consisting of a bear approaching or following people and entering camp, and only 8% of interactions involved a bear acting aggressively. Nevertheless, the authors concluded that bears were more likely to approach people in developed areas like camps or along roads than when people were hiking in the back country (Albert and Bowyer 1991).

Bears were subject to substantial human-caused mortality whether they were hunted or not (McLellan et al. 1999). The Yellowstone brown bear population experienced a gradually increasing level of human-caused mortality over the past 2 decades as populations increased (Schwartz et al. 2004). During 1993 to 2003, a total of 116 bears were killed, 51 in removal from developments, 30 in self-defense, 17 in illegal killings, 10 for livestock depredations, and 8 in instances involving brown bears mistaken for black bears. During this period, female mortality exceeded 30% of the total mortality in 3 of the 11 years, all prior to 2000.

Injuries from brown bears were reduced in Yellowstone National Park during the 20th century (1930 to 1990s), attributed to storing food and garbage in ways less accessible to bears (Gunther 1994). Aumiller and Matt (1994) reported that in 21 years of managing McNeil River State Park for non-consumptive use of bears, bear viewing doubled, no bear had to be removed from the park, and no people were injured. Combinations of hunter harvest and direct control of problem bears by authorities are the management approaches that have a long history of implementation and will continue to be used.

PREDATOR MANAGEMENT TO BENEFIT SMALL, ISOLATED POPULATIONS

Desert Bighorn Sheep

Small populations of ungulates can be limited and particularly vulnerable to reductions in numbers by predation (Arrington and Edwards

1951). Isolated, small populations of desert bighorn sheep (*Ovis canadensis nelsoni*) have been subject to heavy predation by mountain lions in the past 2 decades (Kamler et al. 2002, Hall et al. 2004, Rominger et al. 2004, McKinney et al. 2006). Declines in bighorn sheep began in Arizona in the 1990s, shortly after declines in mule deer populations in the late 1980s (Kamler et al. 2002). Mountain lions began to prey more heavily on bighorn sheep as mule deer declined. Historically, mountain lion predation on bighorn sheep may have fluctuated along with changes in mule deer populations (Kamler et al. 2002). However, predation on small isolated populations could significantly reduce numbers to low levels that could jeopardize population persistence and require reductions in mountain lion numbers (Wehausen 1996).

Efforts to reduce mountain lion predation on federally endangered Sierra bighorn (*Ovis canadensis sierra*) in California involved removal of predatory lions (Stephenson 2009, personal communication). This amounted to the removal of 1 mountain lion per year and has received support from the public. The strategy reduced predation on these sheep.

Population declines of state-endangered desert bighorn in New Mexico were attributable to mountain lion predation (Rominger et al. 2004) and resulted in removal of 98 mountain lions over 8 years from 4 different populations. Survival rates of lambs improved and the desert bighorn sheep population increased and was down-listed from endangered to threatened status by New Mexico (Rominger and Goldstein 2007, Rominger 2009). The ability of mountain lions to switch prey to domestic livestock, especially calves, may help explain why mountain lion numbers did not decline in the presence of very low wild ungulate densities (Rominger et al. 2004). Additionally, drought that caused declines in mule deer affected mountain lion predation on bighorn (Logan and Sweanor 2001).

Mountain lion populations have been increasing in Arizona and site-specific management plans for the Kofa and Black Mountains have been developed (Thompson et al. 2008), where multiple bag limits and year-long hunts have been instituted. Three lions were removed from the Kofa and Black Mountains in 2007 in an effort to stop the decline in bighorn sheep populations, but no responses of sheep to these actions have been reported.

Experience in Texas has shown how efforts to reduce mountain lion predation will vary depending upon size of area and circumstances in adjacent areas (Richardson, 2008, personal communication). Efforts to restore bighorn in Black Gap Wildlife Management Area (WMA) were hindered by the large size (42,900 ha) of the area and the presence of lion populations in adjacent Mexico that moved into the sheep range. However, the Sierra Diablo WMA, which was less than 4,860 ha and surrounded by private lands where predator control was routine, had a bighorn population of >900. A similar situation occurred in the Elephant Mountain WMA, where predator management, water development, and habitat management including prescribed burning were part of management. Aggressive removal of exotic wildlife that competed with bighorn was also practiced. Mountain lions have never been granted big game animal status in Texas, and year-round trapping and snaring occurred on private and some public lands. Texas did not require pelt-tagging, so estimates of harvest from various means was not known. The distribution of lions in Texas has been the same for the last 25 years.

These examples suggest that selective removal of mountain lions for a limited time can be effective in increasing bighorn sheep survival and ultimately population sizes, but these outcomes will depend upon size of area, location, and management in adjacent areas. Bender and Weisenberger (2005) concluded that precipitation and prolonged drought were also correlated with desert bighorn sheep population dynamics and needed to be factored into efforts to restore and recover populations. During the 1990s, which had mostly below-average precipitation, desert bighorn sheep populations in Texas and New Mexico increased but Arizona populations declined. The differences were assumed to be a function of lion control, but differences in population size and distribution were involved.

Arizona has had more desert bighorn sheep for a longer period of time than either New Mexico or Texas. Provision of artificial water in sustaining both mountain lions and deer was also a factor in Arizona (Cain et al. 2008).

Caribou at the Southern Limits of Their Range

Woodland caribou in Canada were listed as threatened in 2002 (COSEWIC 2002) and as endangered in the contiguous U.S. in 1983 (U.S. Fish and Wildlife Service 1994). Bergerud (2006) elaborated on the effects of predation on isolated caribou populations at the southern limits of their range. A caribou population in Pukaskwa National Park, Ontario, existed at low density in a system that included wolves, black bears, lynx, and moose. On the Slate and Pic Islands (Ferguson et al. 1988), caribou existed at higher densities and were regulated by their interactions with the forage base in the absence of predators. Wittmer et al. (2005) reported declining populations of caribou in the southern mountains of British Columbia. The mountain caribou that existed along the British Columbia-Idaho-Washington border in the southern Selkirks have persisted at less than 50 animals over at least the past 5 decades, with predation by mountain lions implicated in suppressing population growth. During these decades, the population was augmented with >100 caribou from British Columbia and predation by mountain lions was implicated in suppressing population growth (Wielgus et al. 2009).

Some mainland caribou populations have been isolated through logging and other developments that reduced habitat availability (Edmonds 1988, Rettie and Messier 1998, Boisjoly et al. 2010). In these instances, predation can suppress population growth because individuals are confined to habitat fragments, especially in winter. As logging increased, creating habitat for elk, mule deer, and moose in areas close to caribou, the predators that followed also preyed on caribou and suppressed or retained populations at low density even when more habitat was available (Seip 1992, Rettie and Messier 1998, Wielgus et al. 2009, Latham et al. 2011). McNay et al. (2008) recognized that measures to reverse widespread declines in woodland caribou must involve mitigation of predation by a combination of comprehensive strategies including managing habitats, access, and ungulates as well as the predators.

Caribou populations in northeastern BC increased following reductions in wolves (Bergerud and Elliott 1986). Approximately 996 wolves were removed from 1978 to 1987 (National Research Council 1997). This resulted in increases of caribou, moose, and stone sheep, based on available census data. When wolf control ended, wolf populations increased from 4.6 wolves/100 km^2 to 12.6 wolves/100 km^2 one year later, likely due to immigration. Concerns in the region centered around increased moose and elk populations resulting from habitat improvements attributable to fire (Lousier et al. 2009) and logging, which have caused wolf populations to expand and more effectively prey on caribou (Thiessen, BC Environment 2009, personal communication). Gustine et al. (2006) reported that estimates of predation risk for woodland caribou in this ecosystem were highly variable in different vegetative communities, which suggested that an adaptation to a large number of vegetative conditions was related to the presence of predators.

A similar pattern involving coyote predation on an isolated population of Gaspésie caribou in Quebec was reported by Boisjoly et al. (2010). Coyote population increases within the range of this endangered population of caribou were related to logging activities that promoted increases in moose, berries, and snowshoe hares. Coyotes were initially observed on the Gaspésie Peninsula in 1973 and have expanded their range into boreal forest following logging.

Black-tailed Deer on Vancouver Island

Janz and Hatter (1986) reported a situation involving black-tailed deer (*O. hemionus columbianus*), wolves, and changing habitat on Vancouver Island. Deer concentrate their use of mature forest during periods of deep snows. When these forests are logged, increased forage develops that can be used when snow conditions allow, but confinement to smaller patches of suitable winter habitat during severe winter conditions increases vulnerability to wolf predation. Wolf populations increased rapidly in the late 1970s following an influx of wolves from the adjacent mainland that took advantage of increased deer populations. As a result of increased predation by wolves, deer populations in some watersheds declined 50-70% between 1976 and 1982. Hunter harvest declined from 23-75% depending upon the individual management unit. A wolf control program conducted during 1983 to 1990 on a drainage in the northern part of the island caused deer numbers to increase from an estimated 6,760 to 22,070 individuals (Hatter and Janz 1994). Hunter harvest during the period of wolf control was less than 2% of the deer population with no antlerless harvest. A model proposed that control programs resulting in reductions of approximately 40% in wolves could initiate increases in black-tailed deer that would double the population size in approximately 10 years (Hatter 1988).

Subsequently, wolf management on Vancouver Island has been primarily through legal trapping, which has tended to minimize the potential for major increases in wolf abundance. Wolf numbers have been relatively stable since this earlier work (Brunt 2009, personal communication) Following declines in deer on the island in the 1990s, deer have been generally increasing. The decline during the 1990s coincided with increasing mountain lion populations, which have since stabilized at relatively lower levels.

WOLF AND BEAR CONTROL TO ENHANCE UNGULATE POPULATIONS IN ALASKA

Management of predators is highly controversial in Alaska. Political involvement in predator management preceded Alaska statehood (Regelin 2002, Van Ballenberghe 2006). A National Research Council report (National Research Council 1997) concluded that many of the early predator control programs had unclear results because of faulty experimental design and monitoring, spurring ADFG to better evaluate and execute control programs. However, the combination of political and scientific issues that were involved made it inevitable that controversy would continue.

The Alaska Intensive Management Law of 1994 required the Alaska Board of Game to identify moose and caribou populations that were especially important food sources for Alaskans and ensure that populations remained large enough to allow for adequate and sustained harvests. Proposals for intensive management were subject to public review through local area advisory committees and open meetings of the Board of Game in regional population centers. ADFG reviewed biological parameters including the nutritional and reproductive condition of the ungulate population, condition and capability of the habitat, climatic considerations, harvest and population objectives, subsistence needs, access, and other factors. Plans were developed and reviewed and adaptive management plans are being developed for new programs. Despite this extensive public involvement and biological review, intensive management programs remained controversial.

Ungulates, particularly moose and caribou, are important sources of food for Alaskans, and active predator reduction programs have been established where public hunting and trapping of predators have been unsuccessful in reducing predation on moose or caribou (Titus 2009). Each of these areas has a unique combination of predator and prey populations and habitat characteristics. Alaska's control programs occurred on about 9% of the total land area, but essentially most of the interior part of the state had liberalized regulations involving harvest of wolves and bears. In some areas, black bear females with dependent cubs have been killed, and gassing of wolf pups in dens has also occurred.

Public hunting and trapping of wolves, aerial shooting with same-day airborne takings, land-and-shoot harvest of wolves by permittees, and use of snow machines were methods of reducing wolves, depending upon the specific area and circumstances. Specific goals for reduction of wolves and bears were developed.

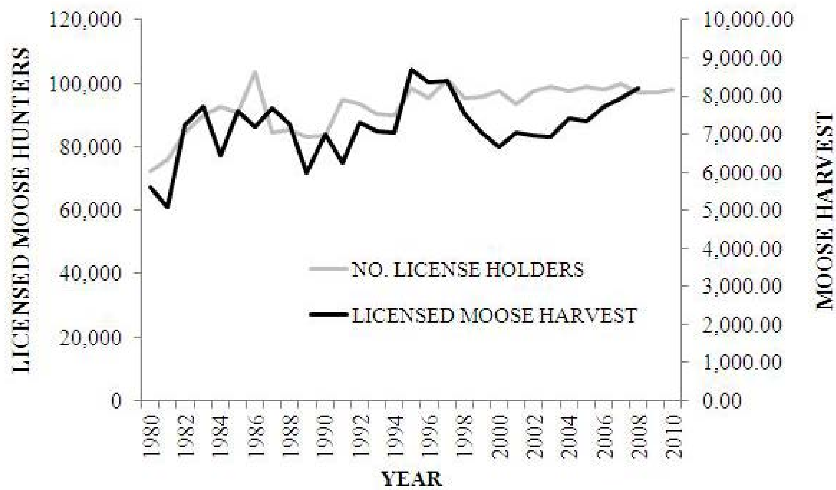

Figure 11. Moose harvests and hunter numbers in Alaska, 1980-2009.

ADFG has issued emergency orders to close the control program to prevent reduction of wolf populations below mandated objectives. In all cases, improvement in either calf survival or population sizes were recorded. Also, ungulate populations involved have been considered to be below KCC based on measures of body condition, reproductive rates, and forage assessments, suggesting that the habitat could support more animals. Wolf harvest was low when snow conditions were unsuitable for effectively tracking wolves in more open habitats.

Public participation in bear control areas that did not adequately reduce bear populations led to additional bag limits and methods of harvest. Black bear seasons were extended and bag limits increased in other areas. In one area, a group of organized sportsmen made a concerted effort to sustain black bear harvest by keeping a sequence of hunters observing baits on a 24-hour basis. Sales of black bear hides and skulls by permittees are used to encourage reductions of predators in another area. Taking of females and cubs was authorized.

Miller et al. (2011) reported on significant increases in general hunting regulations for brown bears and corresponding increases in harvests in 76% of Alaska, motivated largely by regulations designed to reduce bear abundance and thereby increase ungulate harvest for hunters. The grizzly harvest in interior Alaska increased from 392 in 1980 to 781 in 2006. Snaring of grizzly bears was also authorized in some areas in an effort to further reduce populations.

The statewide harvest of moose increased from 1980 to 2009, with most of the increase occurring since 2000 (Figure 11). Hunter numbers fluctuated from 1980 to 2009 with a slightly increasing trend. Highs in 1984 and 1996 were related to expanded caribou hunting opportunities rather than changes in moose hunting opportunity. Moose harvest was weakly correlated with the increase in hunter numbers from 1980 to 2009, but not from 2000 to 2009. The evidence suggests that because hunter numbers were not well-correlated with the increase in moose harvest over the last decade, efforts to increase moose harvest by reducing predation contributed to increased statewide moose harvest in Alaska in recent years. However, high harvests in the mid-1990s and some years in the 1980s suggested that hunting conditions affected the harvest as well.

Successful Wolf Control to Increase Ungulates

The National Research Council (1997) review of predator control programs in Alaska concluded that wolf control could be successful in increasing prey populations and harvest where a high proportion of the wolf population was reduced over a large area for 4 or more years. A successful wolf control program of that type (1976 to 1982) in the Tanana Flats/Alaska Range foothills (13,444 km^2) produced lasting effects in the moose population (Boertje et al. 2009). Moose calf, yearling, and adult survival increased simultaneously, which indicated wolf predation limited the moose population prior to wolf control (Gasaway et al. 1983). Bear predation on moose calves was less limiting than in other areas of Alaska (Boertje et al. 2009). Moose numbers increased 7-fold over the next 28 years. Ground-based wolf control conducted in 1993 to 1994 to benefit the declining Delta caribou herd was halted prematurely but likely benefited the moose population, which had experienced several severe winters. Harvest averaged 5% of the pre-hunt population from 1996 to 2004, the highest sustained harvest density recorded in interior Alaska for similar-sized areas (Boertje et al. 2009). During this same period, harvests ranged from 2-3% among low-density, predator-limited moose populations elsewhere in interior Alaska. From 2004 to 2006, harvest increased to 7% to reduce the population to improve reproductive rates and reduce the moose population to meet management objectives (Boertje et al. 2009). Despite predation and low moose reproduction, continued high human harvests were maintained due to high moose density, a sustainable harvest of cow moose, and consistently favorable weather (Boertje et al. 2009). Only 2 years of wolf reduction have occurred since 1982, and wolves, black bears, and brown bears are abundant. The moose population is currently limited by a combination of predation, food regulation, and human harvest.

Young et al. (2006) and Young and Boertje (2004) concluded that managing moose for high harvests immediately south of Fairbanks reduced demands for predator control, fulfilled legal mandates, and increased public support for protecting and enhancing moose habitat. During the last decades, 2 large wildland fires were allowed to burn, providing effective habitat improvement in important areas of the unit. Disturbance such as fire is critical to maintaining high-quality habitat for moose. Without public support for maintaining moose as a resource, such fires would have been extinguished to prevent smoke and property damage. Difficulties in managing the population include defending antlerless moose hunts to the public, maintaining a complex zone-based management system, and dealing with increased conflicts among local and non-local users (Boertje et al. 2010).

Unit 16B and a small portion of 16A were designated as intensive predator management units with the goal of reducing predators as a means of increasing moose calf survival and ultimately moose harvests (Alaska Board of Game 2011). Immediately west of the Cook Inlet, these units are popular hunts for people from the Anchorage and Matanuska-Susitna Valley areas and residents of villages in the units. In 2004, wolf harvest and control activities began in a portion of unit 16A, resulting in 115 wolves killed in 2004-2005. Declining harvests followed, with 40+ wolves in 2005-2006 and 2006-2007, 30+ wolves in 2007-2008 and 2008-2009, and <10 wolves in 2009-2010 and 2010-2011. Fall wolf population estimates were 180 to 200 in 2004-2005 and dropped to 67 to 105 in 2010-2011. Black bear seasons were liberalized in 2008 to include snaring of all age classes and sexes. No bag limits or closed seasons were in force. Applications for snaring control resulted in 7 permits in 2009 and 14 in 2010, with 77 bears snared in 2009 and 62 in 2010. An average of 520 black bears per year was harvested by general harvest and control methods from 2008 thru 2010. At a meeting on 10 March 2011, the Board of Game authorized baiting and snaring of brown bears in one experimental area, known to be a major mortality factor to moose calves.

Current moose population estimates are 8,434 moose, considered to be below the forage-based carrying capacity for both units as evidenced by the high twinning rates (50%), high pregnancy rates for young animals, autumn and spring calf mass, and autumn and spring rump fat on adult females. Unit 16A had low harvest but high hunting pressure due to access, while unit 16B had both low populations and harvest, increasing in portions of the unit. Road-caused mortality of moose has varied between 200 and 400 moose since 2003.

The fall census for unit 16B has been divided into southern, middle, and northern segments of the unit plus a census of Kalgin Island. Except for a decline in the middle census segment from 3,314 moose in 1999 to 1,836 in 2001, as of 2008 there was no trend in the data. Hunter harvest from 1997-2007 declined from 377 in 1997 to a low of 144 in 2002, increasing to 272 in 2003, then declining again to 258 in 2004, 199 in 2005, and 168 in 2006. Variation in hunter harvest since 2002 is largely due to adjustments in season and bag limits. Only limited subsistence harvests were conducted in most recent years. The average moose harvest over the 10-year period was 270 in unit 16B. At this point, predator control efforts have not appeared to alter moose population trends in unit 16B. Survival for animals greater than 4 months of age is very high and higher than pre-control levels, but survival of neonates remains poor. Survival from birth to 4 months has ranged from 6-24% (mean 14.7%) since approximately 70% of the total summer mortality is caused by black and brown bears.

DESIGN AND IMPLEMENTATION OF PREDATOR CONTROL PROGRAMS

Past predator management efforts were often not conducted with the level of rigor necessary to provide broad insight into the role of predation in limiting (or regulating) ungulate populations (National Research Council 1997). Since that time, extensive information has been developed that has addressed that problem in Alaska and elsewhere. While there is rich theoretical literature to draw upon in terms of understanding predator-prey interactions and predicting outcomes of predator removal, predator control efforts usually are designed with the primary objective of reducing predator numbers in an attempt to recover prey populations for human harvest rather than providing insight into predation's impact on ungulate populations. The 12 large carnivore control studies reviewed by the National Research Council (1997) were each initiated specifically due to the perception that predator removal would increase ungulate densities and hunter success. Although ungulate populations were monitored prior to reaching the conclusion that predator removal was required to increase ungulate population densities, in general studies tended to lack a robust experimental design necessary to attribute prey demographic change specifically to management actions. There are 8 primary problems associated with predator control studies:

1. Lack of spatial or temporal replication of predator removal as well as lack of control sites for assessing baseline changes in population demographics. This leads to weak or no statistical power and difficulties establishing a cause-and-effect relationship between predator removal and ungulate population change. Alternate study designs are available to address the limitations imposed by most predator control studies (National Research Council 1997).

2. Predator removals that are focused on single species (e.g., wolves) and no effective reduction of numbers of other predators (e.g., bears or mountain lions). Direct effects of other predators may not be well understood concurrent with predator control, leaving open the possibility for compensatory predatory responses by other predators that are difficult to quantify.

3. Cessation of hunting activities during periods of predator removal. Although it is understandable that at low ungulate densities there would be a desire to curtail human harvest, this situation confounds the interpretation of any prey demographic change following predator removal.

4. Failure to adequately document ungulate habitat quality prior to predator removal. This causes uncertainty regarding whether the habitat can realistically support increased prey numbers following predator removal, and can lead to equivocal results

of predator removal if ungulate populations are then limited by low-quality habitat. This applies to all jurisdictions, but the NRC 1997 review commissioned by the Governor of Alaska was conducted after a long period of very little predator control. Most of the programs reviewed were conducted in the 1970s and early 1980s.

5. Duration of predator control activities that is too short to affect the required change in predator numbers. Predator control may need to be maintained over the long term to sustain any demographic benefits to ungulate populations. However, intensive control of large mammalian predators is rarely socially sustainable over the longer term (Boertje et al. 2010).

6. Inadequate estimation of predator densities before and/or after the removal. The lack of data makes it difficult to rigorously estimate the magnitude of predator population change due to control actions, and thus leaves unclear the level of predator control associated with the observed effect on ungulate populations. In addition, failure to document whether any remaining predators are local recruits vs. new immigrants weakens mechanistic explanations for how predator populations respond to control.

7. Failure to adequately monitor prey demographic change following predator removal. Predator removal studies usually rely on short-term indirect methods of documenting ungulate population response (e.g., changes in survival, recruitment, adult population size, or calf:cow ratios), but rarely collect direct and sustained measures of ungulate population density.

8. Lack of a quantitative statement as to what constitutes successful vs. unsuccessful predator removal. Predictive models should be developed *a priori* to elucidate likely ungulate population and hunting success responses given a range of predator removal levels, as well as consider other relevant factors such as potential compensation by remaining predators, immigration by new predators, increased local recruitment of predators, changes in habitat quality following ungulate population response, and sustainable levels of hunting. Such models should be important in the formal development of study objectives and endpoints, and provide a further means of defending predator control studies against criticism.

The above list of shortcomings is not entirely surprising given the expense and difficulty of working on free-ranging carnivores at large spatial scales required to influence ungulate populations. Political considerations that influence management decisions may override research needs regarding predator management, leading to compromised research design and implementation in favor of public support and perception. For example, although aerial control is the most effective means of wolf removal and population reduction, this method is not viewed as a favorable means of control by the public and is frequently replaced with less-effective methods. However, alternative methods such as ground-based control, sterilization, or diversionary feeding are less effective and inevitably lead to predator management studies having weak results regarding the role of predation on ungulate populations (Hayes 2010). Ultimately, such shortcomings limit the value of previous predator control studies in providing a reliable knowledge base for predator management, and thereby increase the likelihood that predator control efforts are implemented in situations where baseline information would suggest that such efforts are unlikely to be successful.

Control of large predators may benefit from closer attention to existing theoretical and empirical work on predator-prey interactions in other systems, as well as sounder experimental design and implementation of the studies themselves. Increased attention should be afforded to developing *a priori* predictions, modeling alternate response scenarios, and establishing clear endpoints. The Alaska experience suggests that a comprehensive evaluation can result in better information-gathering and understanding of predator-prey systems, and should be applied more frequently elsewhere.

RECOMMENDATIONS

Predator management is a complex issue without an appropriate, uniform approach that can be applied across regions and species. Policies regarding predators differ by state/province and agency and vary in their impacts on strategies available to managers to address predator conflicts. This review has compiled data that can assist managers in the decision-making process, including the following overarching recommendations that should be considered for the effective management of large mammalian carnivores:

1. Public education programs—designed to inform the public of ways to minimize damages from large mammalian carnivores—can help maintain some level of public tolerance for these species.

2. If managers want to reduce human-predator conflicts, measures should be taken to deter predators from associating people and dwellings with food and, when appropriate, limit human access to areas occupied by predators. Trapping, calling, and shooting are some strategies that have aided in retaining fear of humans in coyotes and are also applicable to bears, wolves, and mountain lions.

3. A well-designed, science-based analysis of predation pressure should be completed prior to initiating predator control. Coordination between state and provincial agencies can facilitate better understanding of a predator species' current status in an area and lead to appropriate management actions.

4. Wildlife management agencies should be transparent in communicating with the public about predator control activities. If managers choose to use adaptive management, they should advise the public of the uncertain outcomes of their activities in producing intended results and they should document all aspects of the situation as completely as possible.

5. Agencies should set appropriate harvest objectives and methods to regulate predator density and distribution. In the case of wolves, population regulation should attempt to focus harvests in areas where conflicts between wolves and ranching operations occur and in areas where increases of target prey species are desired. Consideration of predator biology and public sentiment towards predator harvest regulations by managers can aid in maximizing recreational value of harvests, minimizing public animosity, and accomplishing population management objectives (Mech 2010).

6. Further investigation is needed to examine whether hunter harvest can be an effective and economical substitute for agency control efforts. If public hunting is substituted for agency control efforts, highly regulated and monitored forms of harvest must be employed, including sometimes giving preference to targeting problem individuals of a predator species. In addition, the affected public must be adequately advised, and hunter behavior must be well regulated.

7. Predator management studies in the past have tended to lack a robust experimental design necessary to attribute changes in prey demographics specific to management actions. Future research should use strong and valid experimental designs that enhance understanding of prey and predator species, their interactions, and their relationship to the landscape.

8. Managers should consider estimates of prey populations and trends, condition of prey, its habitat, and effects of severe winters or prolonged drought when determining if certain actions to manage predators are warranted. When habitat conditions are implicated in exacerbating conflicts between humans and predators, interdisciplinary approaches to obtaining information may be useful, and an assessment of effects of

habitat condition on higher trophic levels is necessary to develop ungulate harvest objectives, evaluate ungulate populations, and more fully understand predator-prey dynamics. If nutritional status of individuals is to be used as a primary indicator of habitat condition relative to population size, those parameters need to be measured over extended periods of time.

CONCLUSION

Management of large mammalian carnivores involves finding a balance between maintaining viable carnivore populations, safeguarding human welfare and property, and satisfying the needs of stakeholders in a cost-effective manner. Human expansion into carnivore habitat has been a major cause of increased conflict and mortality for predators. Societal attitudes towards these species are complex and variable. Those who suffer predator damage to property or loss of opportunity to hunt game species preyed upon by predators are more likely to support reductions than those who are little or unaffected by predators' presence. Wildlife management agencies will continue to deal with this range of attitudes. Increased attention on large mammalian carnivores means that justification for management actions must depend on reliable information that is skillfully articulated to a concerned public.

Until recently, wolf population increases in Alaska after 1970 could be attributed to reduced control measures and retention of adequate populations of caribou and moose, which suggests that appropriate habitats were generally being maintained. Current regulations that were intended to maximize human harvest and minimize other causes of ungulate mortality may reduce predator populations to unnecessarily low levels resulting in increased ungulate pressures on available forage.

Brown bear populations in the Yukon and BC appear to be either stable or increasing. Harvest of brown bears in BC has declined with a subsequent decline in damage to life and property. Reductions in damage have been attributed to more effective efforts to inform the public about steps needed to reduce damages. A measure of success of the recovery programs for brown bears will be when regulated hunter harvest can again occur. Efforts in Alaska to reduce predation on ungulates by brown bears need to consider retention of populations at some level that does not cause local extirpations for extended periods. Alaskan law dictates that bears, and other wildlife, be managed on a sustained-yield basis, and Alaska Department of Fish and Game programs are specifically designed to meet that mandate even during population reductions. No local extirpations of black or brown bears have been proposed or have occurred.

Black bears have expanded their range in the eastern parts of the continent. Additionally, they are efficient predators on ungulates in some circumstances. As populations have increased, so has damage to life and property in the western ranges. Restoration of black bears to available habitat has largely occurred except in portions of the southeastern U.S. Hunter harvest is the most efficient means of managing populations, but it is unlikely that hunters will be able to reduce depredations in areas where human habitations are prevalent and tolerance of hunting is low. The tolerance of hunting black bears is also related to means of harvest. When females and cubs are harvested, public tolerance of hunting tends to be low. Errington (1947) observed a tendency to overdo the control and killing of predators whenever they were perceived to have an influence on more desirable wildlife species, and this tendency appears to be happening with black bears in some situations.

The high level of mountain lion harvests in the 1990s appeared to reflect increased populations that have since declined. Investigations of bighorn sheep in the southwestern U.S. implicated predation by mountain lions in affecting populations. A prolonged drought in the region likely exacerbated or may have been the ultimate cause of the declines. Reduction of mountain lions in the northern portions of their range through liberalized harvest with the desired intent of benefiting their ungulate prey has little scientific support, and needs more investigation.

The increased politicization of predator management means that as political regimes change, predator management policies change and wildlife management agencies adjust to these changes. Often, attempts to document what is actually happening are made after the controversies heighten. Many investigations involve marking a number of young of whatever prey species is of concern and recording what happens to the marked sample. Almost without exception, these investigations reveal that most mortality is attributable to predation. Estimates of prey populations and trends may also be involved, because this is commonly obtained through routine monitoring of ungulates. The connection between predator and prey is oversimplified through this approach, however, especially when it only lasts a few years. Predation on ungulates is an expected major cause of mortality, outside of human harvest. The degree to which predators kill enough individuals to cause reductions in breeding stock is highly variable. Efforts to coordinate hunter harvest levels with predation levels are always difficult and are largely inadequate. Due to increasing workloads and reductions in available state agency personnel, wildlife managers often do not have adequate time to attempt further explanations that invariably are more complex and may appear to obscure the issue. More important, management decisions often have to be made with the best available science at the time issues arise.

Traditional funding mechanisms for wildlife management and conservation, based on the user-pay-user-benefit model, greatly affect how predator management is pursued at the state level. Although the Public Trust Doctrine for Wildlife Management clearly articulates that state and federal agencies manage wildlife for the benefit of all citizens, often the opinions of non-consumptive users are ignored. Unbalanced information that supports the perceptions of some stakeholders over others can increase conflicts. In states and provinces that are highly urbanized, voters that are unaffected by carnivores can simply outvote those who are affected. Conversely, where agricultural and rural interests prevail on the political scene, carnivores can be reduced to levels that are well below those needed to sustain populations.

Another major problem is evaluating habitat relationships for ungulates. Estimates of KCC on a given landscape show that fluctuations depend in part upon rainfall and snow, which make such estimates tedious to obtain at best. Direct examinations of ungulate conditions such as those provided by Boertje et al. (2007) may not provide evidence concerning habitat condition, given the extreme adaptability that these species show in forage choice and distribution in naturally fluctuating environments. If habitat conditions are excellent, precipitation patterns can still be variable enough to cause significant changes in KCC. Knowledge of plant succession following fire or logging, and responses of individual forage species to different levels of herbivory, may require expertise that wildlife biologists concerned with the predator-prey relationship may lack. Additionally, when prescriptions for using fire and logging to improve habitat for ungulate prey are anticipated, expertise in managing these activities may require other resource specialists.

The tendency to maintain high ungulate populations as a matter of public preference, with exceptions such as white-tailed deer in urban and suburban areas, also means that the forage base will be more likely to influence population performance during periods of stress, especially where ungulate populations exhibit strong density dependence. Such populations will obviously support higher numbers of predators and create situations where predator control is demanded. Mule deer populations at high levels may not respond to reductions in their predators (Ballard et al. 2001). An artificial winter feeding program increased overwinter survival of mule deer fawns and adult females and reduced predation rates (Bishop et al. 2009). Post and Stenseth (1998) concluded that rates of increase of moose and white-tailed deer were variable depending upon winter severity, global climatic variation with 2 and 3 year lags, density-dependent feedback, and wolf predation. Knowledge of population size relative to nutrient and climate change is critical to understanding whether predator control will be of value. When habitat is created as through wildfire or other means, populations at low density may be slow in responding to improved forage conditions because of predation.

A direct examination of forage conditions is necessary to assess effects of populations on habitat, especially for ungulates that rely on late-succession foraging conditions. For ungulates that rely on early-succession conditions, habitat forage capability declines through time regardless of population size. Disturbance, such as flooding and ice scarification of river bars, wildland fire, or human manipulation has a greater effect on long-term habitat capability than foraging pressure.

The situation involving desert bighorn sheep and mountain lions in the southwestern U.S. illustrated a practical application of short term predator reductions that was justifiable. In this case, prolonged drought likely contributed to increased mountain lion predation on desert bighorn as vulnerability of other prey species declined. Isolated caribou populations along their southern range where habitat fragmentation is occurring represent another situation where predator management is appropriate if these populations are to be maintained (McNay et al. 2008).

Predators commonly occur in multiple-use areas that emphasize management of natural resources and allow extensive human activity. These predators should be managed at levels that ensure their retention on the landscape at levels that are compatible with other land uses. Such areas may be in public or private ownership and are often in combinations. Efforts to minimize depredations on livestock and other property are routinely accomplished and, especially in the case of wolves and livestock, new approaches are being tried with some success.

Agreements between the U.S. Forest Service (USFS) and state wildlife agencies concerning management of wildlife in Wilderness Areas (International Association of Fish and Wildlife Administrators 1976) should be examined and revised to provide for harvest of big game populations and their predators at levels that are compatible with wilderness values. In places where human presence and impact is minimized, wildlife populations of all species should be allowed to fluctuate with as little anthropogenic interference as possible. This does not mean that hunting and trapping should be prohibited, but rather that they are pursued at levels that do not unduly influence wildlife. It should be noted that humans historically have been a part of the North American wilderness and undoubtedly have had effects on wildlife populations.

Evidence that predators can reduce ungulate populations to levels that are well below KCC indicates a need to sometimes manage predator populations over extended periods at levels that maintain high populations of ungulate prey where human harvest is important. Bergerud (1988, 2008) and Boertje et al. (1996) recognized that judicious predator management that resulted in higher population levels of prey still compatible with their habitat could result in higher population levels of predators than would be sustained if their prey remained at lower levels. This illustrates the irony of not using a reliable data base to manage these systems. The proper role for the layman and politician is to hold the professionals accountable, question whether the information being used is adequate or not, be patient with management efforts, recognize that management has to adapt to complex, changing circumstances, and provide resources necessary to do an adequate job of monitoring predators, prey, and habitat. This is the ideal to be strived for, in full recognition that human emotions and convictions must be considered in the never-ending effort to better understand the natural world. Perhaps this is the ultimate challenge that management and conservation of the large mammalian predators provides humanity and wildlife management.

Wildlife resources are a public benefit, and wildlife biologists typically advise policy and decision makers concerning management. As a result, practices that are viewed as indefensible to some are supported or at least acceptable to others. Nowhere is this more apparent than in the management and conservation of large predators. For example, Boertje et al. (2010) advocated that reducing wolves and bears to low densities could enhance harvest of moose and caribou in Alaska. Hayes (2010), using a similar data set, concluded that reducing wolves using traditional methods was not appropriate for the Yukon Territory.

It is imperative to recognize that the knowledge base and data set alone cannot determine whether management or control of large carnivores is warranted. Rather, the role of science is to predict and evaluate the outcomes of such management. The decision to manage large carnivores will largely be driven by human values and the circumstances under which those values are tested against other values. Large carnivores can constitute a threat to human safety, be competitors with people for game resources, be a keystone component of an ecosystem, be an icon of wilderness, and be all of those at the same time. Regardless, this review suggests that large mammalian predators have made a remarkable comeback from the lows of the early 20th century and that a large share of the North American public tolerates their presence and realizes that management at some level is at times necessary.

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APPENDIX. ANALYSES OF TRENDS IN RECORDS USING REGRESSION[1]

RECORD	REGRESSION	TREND	AIC	ΔAICC[2]	AIC Weight	NEXT BEST Model
Alaska black bear DLP vs year(Damage to life and property)	DLP=-3.491(Year)	↑	218.3	3.58	1	lnYear
Alaska black bear harvest	Harvest=-59.686+.0337(YEAR)	↑	379.79	4.78	0.916	lnYear
Alaska black bear harvest vs DLP	Harvest = 3.491(Year)	↔	218.297	11.231	0.498	lnYear
Alaska brown bear harvest, 1980-2008	Harvest=-50642.07+26.03(YEAR)	↑	399.183	0.2076	0.5258	lnYear
Alaska Grizzly DLP vs year	DLP=-2.44.32+1.057(Year)	↑	-127.84	167.95	1	lnYear
Alaska grizzly harvest related to DLP	DLP=3.845+.00022(lnHarv)	↑	409.045	0.0977	0.497	Harv
Alaska Kodiak Bear Sport Harvest	Harvest = 153.22(Year)	↔	626.064	0	0.451	lnYear
Alaska Kodiak Bear Nonsport Harvest	Harvest =14.672(Year)	↔	415.465	0	0.492	lnYear
Alaska wolf take	Harvest=-46924+24.1538(Year)	↑	337.387	1.312	0.657	lnYear
Alaska moose harvest 1981-2009	Harvest = -78154+42.78(Year)	↑	449.77	0.2824	0.533	lnYear
Alaska moose harvest 1983-2009	Harvest=-33527+20.149(Year)	↑	411.298	1.831	0.784	lnYear
Alaska moose harvest 2000-2009	Harvest =-291500+149.08(Year)	↑	126.932	0.695	0.586	lnYear
Alaska hunter numbers 1980-2009	Hunters = -925919+510.87(Year)	↑	553.488	4.104	0.886	lnYear
Alaska hunter numbers 2000-2009	Hunters=-279117+187.95(Year)	↔	161.404	0.0488	0.493	lnYear
Alaska moose harvest related to hunter numbers 1980-2009	Harvest= 720.07+0.06944(Hunters)	↑	459.09	0.62	0.511	lnHunters
Alaska moose harvest related to hunter numbers 2000-2009	Harvest= -1401.09+0.089(Hunters)	↔	141.56	4.01	0.671	No intercept
Alberta black bear harvest	Harvest =-44526+22.87(Year)	↔	225.58	5.98	0.002	lnYear
Alberta cougar harvest	Harvest = -7777.32+3.932(Year)	↑	144.08	0.012	0.002	lnYear
Alberta mule deer harvest	Harvest=-214511+116.04(Year)	↔	315.26	0.25	0.0022	lnYear
Alberta number of trappers	TOTAL = 155.27-.0738(LNYear)	↓	400.97	1.83	0.011	Year
Alberta wolf harvest, 1989-2008	Harvest=5753.93-2.7382(Year)	↔	215.18	6	0.002	lnYear
APHIS Total US coyote harvest 1998-2008	Take= 4.1+.0036(lnYear)	↔	201.978	0.00213	0.497	Year
APHIS coyote take in Arizona	Take= 128481.01-63.6495(Year)	↓	249.868	0.3154	0.539	lnYear
APHIS coyote take in California	Take=-54687+30.797(year)	↔	300.345	0.00017	0.488	lnYear
APHIS coyote take in Colorado	Take = -2267.227+2.654(Year)	↔	274.527	0.00011	0.473	lnYear
APHIS coyote take in ID	Take = -50734.41+27.982(Year)	↔	294.429	0.01	0.489	lnYear

Continued (2 of 4)

RECORD	REGRESSION	TREND	AIC	ΔAICC[2]	AIC Weight	NEXT BEST Model
APHIS coyote take in MT	Take =-321134+164.67(Year)	↑	293.597	0.8503	0.603	lnYear
APHIS coyote take in New Mexico	Take =377553.09-185.828(Year)	↓	270.723	0.893	0.609	lnYear
APHIS coyote take in NV	Take=-15.66+.012(lnYear)	↔	284.996	0.04351	0.491	Year
APHIS coyote take in OR	Take=404823.98-199.4167(Year)	↓	284.264	2.264	0.756	lnYear
APHIS coyote take in TX	Take=-13.64-.0019(lnYear)	↔	299.209	0.0079	0.49	Year
APHIS coyote take in UT	Take=12.39-.002 (lnYear)	↔	266.043	0	0.469	Year
APHIS coyote take in Washington	Harvest=277755377-138.37(Year)	↓	281.096	1.2563	0.649	lnYear
APHIS coyote take in Wyoming	Harvest=-28.646+.0187(lnYear)	↑	284.257	0.0717	0.506	Year
Black bear harvest in western states except Alaska	Harvest=-118700+61.897(Year)	↑	443.823	2.41	0.769	lnYear
British Columbia black bear harvest 1980-2006	Harvest=12605-4.311(Year)	↔	368.01	6	0.002	lnYear
British Columbia black bear nonresident harvest	Harvest =-73039+37.158(Year)	↑	321.05	6	0.002	lnYear
British Columbia black bear resident harvest	Harvest=85645-41.469(Year)	↓	366.06	6	0.0022	lnYear
British Columbia brown bear harvest 1976-2006 (2001 excluded)	Harvest= 13083-6.4176(Year)	↓	285.523	0.1688	0.521	lnYear
British Columbia cougar harvest(1976-2006)	Harvest=-8851.61+4.542(Year)	↑	345.51	0.96	0.0022	lnYear
British Columbia mule deer harvest	Harvest= 1533878-756.81(Year)	↓	368.53	0.37	0.00219	lnYear
British Columbia mule deer hunters	Harvest=3145970-1547.96(Year)	↓	378.34	0.37	0.0022	lnYear
British Columbia moose harvest	Harvest=252844-121.24(Year)	↓	446.26	2.377	0.766	lnYear
British Columbia wolf harvest(1976-2007)	Harvest=-2038.85+1.26 (Year)	↔	386.6	0.96	0.002	lnYear
Canada Coyote Harvest 1980-2006, Four Western Provinces	Pelts= 12.5224-.00086(Year)	↔	576.029	0.0015	0.498	lnYear
Canada Coyote harvest related to pelt values	Value = 9.9875+.000619(Pelts)	↑	223.628	0	0.419	lnPelts
Canada Coyote pelt value	Value= 50/404-.023(lnYear)		223.11	0.52	0.476	Year
Canada wolf pelt prices	Price = -31730+16.007(Year)	↔	326.13	1.41	0.872	lnYear
Canada wolf pelt prices predicts the take	Price = 537.91-.977(Pelts)	↔	333.302	0.054	0.257	Pelts
Canada wolf take	Pelts= 50.036-.0222(lnYear)	↓	252.119	0.32	0.539	Year
Coyote take in Alberta	Pelts= 20.74-.005(lnYear)	↔	533.14	0.0419	0.502	Year
Coyote take in British Columbia	Pelts = 214005-106.47(Year)	↓	426.58	1.77	0.707	lnYear
Coyote take in Canada	Pelts=2.789+.004(lnYear)	↔	579.053	0.0354	0.503	Year
Coyote take in Manitoba	Pelts=-35.77+.0228(lnYear)	↔	536.69	0.569	0.569	Year
Coyote take in Ontario	Pelts=36172-16.9(Year)	↓	460.214	0.0006	0.475	lnYear
Coyote take in Quebec	Pelts= -71/551+/0399(lnYear)	↑	410.632	2.109	0.742	Year

Continued (3 of 4)

RECORD	REGRESSION	TREND	AIC	ΔAICC²	AIC Weight	NEXT BEST Model
Coyote take in Saskatchewan	Pelts=41.243-.016(lnYear)	↔	490.631	0.3	0.531	lnYear
Maine black bear harvest	Harvest=-1113062+57.934(Year)	↑	336.855	2.34	0.762	lnYear
Maine deer harvest in 15 northern units	Harvest =36534-180.61(Year)	↓	460.553	0	0.999	lnYear
Maine coyote harvest in 15 northern units	Harvest=-89001+45.4232(Year)	↑	402.398	0	0.982	lnYear
Manitoba moose harvest	Harvest=52.414-.0227(lnYear)	↓	386.63	2.52	0.779	Year
Michigan black bear harvest	Harvest = -192949+97.418(Year)	↑	232.371	4.028	0.882	lnYear
Minnesota black bear harvest	Harvest=-193019+98.1423(Year)	↑	360.644	1.7112	0.702	lnYear
Newfoundland moose harvest	Harvest=-804132+0.42(Year)	↑	544.3	11.01	0.996	lnYear
New Brunswick moose harvest	Harvest =-64158+33.12(Year)	↑	408.4	1.79	0.71	lnYear
New Hampshire black bear harvest	Harvest = -41426+20.928(Year)	↑	278.488	0.605	0.575	lnYear
New York black bear harvest	Harvest=-51.59+.029(lnYear)	↑	308.356	0.06	0.506	Year
North Carolina black bear harvest	Harvest = -146249+73.832(Year)	↑	283.215	36.348	1	lnYear
Nova Scotia moose harvest	Harvest=-5.309(lnYear)	↑	227.16	4.389	0.899	Year
NT wolf harvest 1994-2009	Harvest = -899.94-0.3912(Year)	↓	172.676	0.002	0.303	lnYear
NT wolf pelts sold, 1994-2009	Pelts= -2002.09+1.053(Year)	↑	170.712	0.017	0.302	lnYear
NT wolf pelts sold vs harvest	Pelts sold=-2.2-5+0.919(Harvest)	↑	117.06	3.04	0.8	lnPelts
NT wolf pelts sold vs price	Pelts sold=34.839+.00325(Price)	↑	163.372	8.058	0.951	lnPrice
Ontario moose harvest	Harvest=314775-152(Year)	↓	414.53	8.64	0.987	lnYear
Pennsylvania black bear harvest	Harvest=-187387+94.9763(Year)	↑	334.755	9.22	0.99	lnYear
Quebec wolf pelts sold 1983-2008	Pelts=7.493-.0007(lnYear)	↓	284.097	0.0004	0.329	Year
Quebec wolf pelts sold vs price	Harvest = 480.17(Year)	↔	285.42	11.36	0.498	lnYear
Saskatchewan mule deer harvest	Harvest=-127673+68.586(Year)	↔	472.206	0.027	0.498	lnYear
Tennessee black bear harvest	Harvest=-152.82+.079(lnYear)	↑	248.861	2.107	0.741	Year
Utah black bear harvest vs other recorded mortality	Harvest =-152.82+.079(lnYear)	↑	248.86	2.1	0.7414	Year
Utah total black bear harvest	Harvest =-5381.68+2.729(Year)	↑	251.01	2.08	0.681	lnYear
Vermont black bear harvest	Harvest=-26131+13.2777(Year)	↑	275.853	0.366	0.545	lnYear
Virginia black bear harvest	Harvest=-121.7+.064(lnYear)	↑	285.418	8.933	0.987	Year
West Virginia Black bear harvest	Harvest = -214.7+.064(lnYear)	↑	285.42	8.93	0.989	Year
Wisconsin black bear harvest	Harvest = -155821+78.5(Year)	↑	292.389	32.28	1	lnYear
Yukon Grizzly Harvest	Harvest=2191.05-1.057(Year)	↓	244.471	0.411	0.5078	lnYear

Continued (4 of 4)

RECORD	REGRESSION	TREND	AIC	ΔAICC[2]	AIC Weight	NEXT BEST Model
Yukon Moose Harvest	Harvest=29.016-0.011(lnYear)	↓	333.838	1.049	0.628	Year

1 Four models were evaluated: 1 Harvest on year with intercept, 2 Harvest on lnYEAR with intercept, 3 Harvest on Year with no intercept, 4 Harvest on lnYear with no intercept. Proc GLIMMIX in SAS with code provided by Gary White, Colorado State University.