

Chapter 9

Conservation Planning with Large Carnivores and Ungulates in Eastern North America: Learning from the Past to Plan for the Future

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Abstract While large mammals are often important targets of conservation activities in their own right, they can serve as effective tools for designing conservation landscapes and management measures at the human–wildlife interface. This chapter explores the potential role of large mammals in conservation planning in the Northern Appalachians/Acadian ecoregion, exploring two major questions: What can we learn from the past about the status of large mammals and the drivers of change, and what can this knowledge tell us about how both to plan for their continued persistence or recovery and to deploy them to help cover at least some of the needs of other, less visible components of biological diversity? An analysis of the individual trajectories of 10 large mammal species over the past four centuries of landscape and climate changes in the Northern Appalachian/Acadian ecoregion reveals several patterns of decline and recovery having occurred against a backdrop of variable environmental conditions such as land-use change, climate shifts, prevailing human attitudes, and interspecific relationships. Deploying large mammals as conservation planning tools can range from expanding the scale of conservation ambition to guiding the identification of core conservation lands, connectivity within the overall landscape, and thresholds of development intensity.

Keywords Carnivores • Conservation planning • Mammals • Population trends • Ungulates

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9.1 Introduction

In keeping with the principle that an essential goal of conservation planning is safeguarding biological diversity, it is often assumed that the conservation of large-bodied mammals represents the pinnacle of achievement in this endeavor. This is because ensuring for the persistence of such species often constitutes formidable challenges, as judged by the history of large faunal change in Europe and North America over the past 500 years driven by human-mediated stressors. Members of these species can have high demands for space that collide easily with human interests, and their often low reproductive capacity makes it difficult for populations to recover once in decline (Weaver et al. 1996). To add to this natural vulnerability, such species are also highly valued for meat and other products, or maligned as a source of real or perceived threat to human inhabitants. Through force of gun and plow amidst rising industrial societies, large mammal populations, such as ungulates and carnivores, have been generally among those that are the first to dwindle or disappear worldwide (Laliberte and Ripple 2004; Morrison et al. 2007).

The Northern Appalachian/Acadian ecoregion in Northeastern North America has the continent's longest history of European settlement (Whitney 1994). The shifting distributions of large mammal species occupying the same region mirror the trajectory of land conversion and recovery over the past several centuries. Dwelling in a region characterized by topographic and ecological diversity, large mammal fauna have included at one time or another several ungulate species (caribou [*Rangifer tarandus*], moose [*Alces alces*], and white-tailed deer [*Odocoileus virginianus*], with elk [*Cervus elaphus*] and bison [*Bison bison*] on the outskirts) and carnivores (wolves [*Canis lupus* or *lycaon*], black bears [*Ursus americanus*], cougars [*Puma concolor*], wolverines [*Gulo gulo*], lynx [*Lynx canadensis*], bobcat [*Lynx rufus*], and coyotes [*Canis latrans*]). Each species has individual histories and has responded independently to changing climates and landscapes; not one has enjoyed stable population levels or distributions over the past few hundred years. While ultimate factors lie in land shifts stimulated by humans or more natural climatic changes, in many cases it is the biology of the animals themselves and the strength of their interaction with closely related species that have dictated their status at any given time.

A "focal species" approach to conservation planning refers to the process whereby conservation planning is designed in whole or part on the needs of selected species (Ray 2005a). This is accomplished through assessing their potential for recovery and/or continued persistence under various planning designs (Wilson et al. 2009). Deploying species as both targets and tools in conservation planning can be a logical investment of resources as long as the right species are chosen and perceived relationships with ecological processes are tested (Lindenmayer et al. 2002; Chap. 17). Large mammals can offer particular advantages in this regard because their decline or disappearance from an area says a lot about the state of biological diversity in that region (Morrison et al. 2007; Ray 2005a). A retrospective view is helpful in documenting the range of processes that have affected species persistence within a region over time. Information on historical trends can

highlight the drivers behind species-specific relative abundance and distribution patterns. This can help in efforts to select desired and practical conservation goals as well as effective approaches to achieve them (Motzkin and Foster 2004).

In this chapter, I explore the potential role of large mammals in conservation planning in the Northern Appalachians/Acadian ecoregion. I address two major questions: What can we learn from the past about the status of large mammals and the drivers of change? And what can this knowledge tell us about how both to plan for their continued persistence or recovery and to deploy them to help cover at least some of the needs of other, less visible components of biological diversity? This analysis begins with an exploration of the individual histories of ten species of ungulates and carnivores resident in the ecoregion over the past four centuries. After exploring the drivers behind their declines and/or recoveries, the latter half of the chapter discusses lessons learned that are relevant for conservation planning today in this region and beyond.

9.2 Historical Trends and Limiting Factors

This section contains a review what is known about the historical trajectories of relative abundances and distributions of ten ungulates and carnivores in the ecoregion since the time of European settlement (late 1600s). With each species, I explore what is known about the drivers behind their declines and/or recoveries at particular points of time. I also provide information on their current status and discuss the abiotic and biotic factors that are known to limit their distribution.

9.2.1 *Caribou (Rangifer tarandus)*

Caribou have lost almost one-third of their historical North American range from Southern Canada and the lower 48 states of the U.S. (Hummel and Ray 2008). In the mid-1800s, the coniferous forests of Maine, Northern Vermont, New Hampshire, the Gaspé Peninsula and the Atlantic provinces of Canada were all home to caribou populations (Bergerud and Mercer 1989); Grant (1902) claimed caribou never occurred in Northern New York. This species disappeared from the St. Lawrence Valley of Québec, New Hampshire, and Vermont in the middle part of the nineteenth century but was still hunted in Maine in the late 1890s, with the last native caribou recorded in the state in 1905 (Martin 1980, cited in Courtois et al. 2003). Historians in the region speak of the coming and going of caribou in local areas (Krohn 2005; Parker 2004) due to their propensity to move around in the landscape in an unpredictable fashion; there were also known periods of localized abundance. For example, caribou were described as highly abundant in Northern New Brunswick in the 1880s (Parker 2004), and they occurred throughout the southern shore of the St. Lawrence River through the Gaspé Peninsula (Courtois et al. 2003).

Reasons for the precipitous declines of caribou in the Northern Appalachian/Acadian ecoregion, as elsewhere, stemmed from overhunting, the rising tide of white-tailed deer that took advantage of converted landscapes and milder winters in the region, and increased levels of predation that likewise accompanied the extensive habitat changes (Miller et al. 2003). Evidence suggests that caribou distribution extended further south prior to or following the Little Ice Age (1300–1850) (Telfer and Kelsall 1984), such that the range reflected in our historical record most likely represents a maximum range for this northern species (Bergerud and Mercer 1989). In turn, white-tailed deer responded favorably to the warming trend that took place after this period. Although early authors remarked on the ecological incompatibility between caribou and white-tailed deer (e.g., Palmer 1938), the basis for this was not known until the transmission of the meningeal worm (*Paralastrongylus tenius*, a parasite that when transmitted to caribou is 100% fatal [Anderson 1972]), was discovered.

Following localized declines or population fluctuations during the late nineteenth century, caribou largely disappeared from the ecoregion by the early 1900s, persisting only in the Cape Breton highlands of Nova Scotia until 1925 (Kelsall 1984). One remnant population remains today in Gaspésie National Park in Québec, which numbers just 140 individuals (Courtois et al. 2003). Several translocations into the ecoregion took place since the 1920s, but none was successful, primarily because of transmission of meningeal worms from white-tailed deer (Bergerud and Mercer 1989). Although caribou have never been recorded to reoccupy a range from which they have been extirpated, small, isolated populations have been able to persist for some time, often by means of predator control efforts conducted annually (Festa-Bianchet et al. 2010; Hummel and Ray 2008).

While overharvesting was the primary factor for the original decline of caribou on the Gaspé Peninsula, the cause has shifted in recent decades to predation by coyotes and black bears. Since the 1980s, members of the herd have been increasingly confined to high-elevation areas, nearly coincident with the time when coyotes moved into the region (Mosnier et al. 2003). Repeated predator control efforts were made from 1990 to 1996 and again since 2003 and appear to be necessary in order to ensure for the continued survival of this population (Mosnier et al. 2008).

9.2.2 *Moose (Alces alces)*

When European settlers first arrived on the North American continent, moose were abundant throughout most of the East (Alexander 1993; Bontaites and Gustafson 1993; Courtois and Lamontagne 1997). This was in sharp contrast to the status of the same species that once persisted all over Europe but had already experienced widespread declines in the southern half of that continent by the time the first European settlers arrived in North America. Moose are a favored game species wherever they occur, and were relied on by early aboriginal peoples for food, clothing,

and leather products – traditionally hunted in winter when the hide properties and body condition were most favorable (Parker 2004). During the period of unrelenting exploitation, moose were among the principal quarry of the new inhabitants of the New World such that even prior to the emergence of markets, unregulated hunting not only drove population numbers down in some areas but was responsible for the slow retraction of the species' range. Moose were extirpated from Pennsylvania by 1790 (Karns 1997), Massachusetts in the early 1800s (Vecellio et al. 1993), and the Adirondack Mountains in 1861 (Terrie 1993). By the late nineteenth century, numbers of this species were low throughout New England, the Gaspé Peninsula of Québec, and the Maritime provinces (Alexander 1993; Bontaites and Gustafson 1993; Courtois and Lamontagne 1997; Parker 2004). Even in relatively wild areas like New Brunswick, it was increasingly rare to find moose within easy reach of river shores (Parker 2004). In Cape Breton, Nova Scotia, moose were extirpated altogether by the 1800s and never became re-established until introductions in the late 1940s from Alberta (Beazley et al. 2006).

In Nova Scotia and New Brunswick, hunting restrictions allowed for some recovery of moose populations, but this did not last long. By the late 1930s, hunting seasons in both provinces were closed once again (Beazley et al. 2006; Parker 2004). In New England, moose populations remained in a depressed state and confined to a small portion of their former range, and it took almost a century before they demonstrated signs of recovery beginning in the 1970s (Karns 1997).

Although overhunting had for the most part been the principal driver in bringing down moose populations, ending hunting was not generally sufficient for recovery. While the reason for this was unknown at the time, some observers noted that moose declines were coincident with expansion of white-tailed deer (Parker 2004). It was later determined that the same meningeal worm that limited recovery by caribou were also affecting moose. Indeed, moose populations were able to begin to recover again beginning in the 1900s when three conditions were in place: (1) harvest regulations were instated, (2) forest cover returned, and (3) white-tailed deer declined due to occasional severe winters and return of mature forest. Other factors promoting moose recovery in localized areas included forest clearing in patches. This provided young browse and the increase of wetland habitats following the recovery of beaver (*Castor canadensis*) populations, which themselves had been decimated by overharvesting during the preceding centuries (Alexander 1993; Parker 2004).

Currently, moose in the Northern Appalachians are on a trajectory of recovery, with population increases and range reclamation occurring throughout the ecoregion. For example, in Vermont, moose populations were estimated at 200 in 1980 and grew to over 1,500 by 1993 (Alexander 1993). Today, it is estimated at 4,700 in Vermont, covering the majority of the state (Vermont Department of Fish and Wildlife 2009). In New Hampshire, moose were estimated at 500 in 1977, jumped to 1,600 in 1982, 5,000 in 1993 (Bontaites and Gustafson 1993), growing to approximately 7,000 in the state by 2000 (Aldrich and Phippen 2000). In New York, it appears that moose began immigrating into the state in the 1970s from Vermont (Jenkins 2004). Since then, the population has been increasing steadily and is officially estimated at 300–500 animals (NYDEC, New York State

Department of Environmental Conservation 2009). A small population has even become established in Massachusetts (Vecellio et al. 1993).

Within the ecoregion, two areas stand out where moose populations are not recovering: southern Québec and mainland Nova Scotia. In Nova Scotia, moose are by and large confined to the most remote areas in small populations of questionable viability and appear to be functionally isolated from one another with little evidence of genetic exchange (Beazley et al. 2006). The eastern moose from mainland Nova Scotia has been classified as ‘endangered’ under the Nova Scotia Endangered Species Act since 2003.

Residing in boreal forests in North America and conifer-dominated forest systems of the Northern Appalachian/Acadian ecoregion, the primary factors that determine the northern limit of moose distribution are availability of food and cover, while the southern extent of their range is predominantly limited by climate (Karns 1997). Heat is the most critical of factors, with maximum temperatures leading to stress in summer (Karns 1997). Also, the meningeal worm can be a significant mortality factor where the ranges of moose and white-tailed deer overlap. This disease has been responsible for moose population declines where white-tailed deer are able to exist at high densities (e.g., where snow is shallow enough for them to persist during winter [Beazley et al. 2006]). Unlike caribou, however, moose can co-exist with low-density white-tailed deer populations.

In the northern stronghold of their range, moose are not particularly averse to humans, living in areas that have been settled by humans for long periods of time and flourishing where heavy and repeated logging activity has occurred. However, towards the southern limit of their distribution, such as the Northern Appalachians, it appears that this species has a lower threshold of human disturbance. Most mortality among moose populations in the region is due to vehicle collisions, followed by hunting and meningeal worm (Alexander 1993). Radio-collared moose have been shown to avoid highways at coarse scales of habitat selection (Laurian et al. 2008). Although they are able to adapt to disturbances that are predictable and do not pose any particular threat to individuals, moose tend to avoid areas that are used regularly by cross-country skiers, snowmobilers, and hunters (Forman et al. 1997). Where such uses are squeezed into a relatively small area, such as Nova Scotia, the St. Lawrence Valley of southern Québec, or Southern New England and New York outside of the Adirondack Mountains (Hicks 1986), moose populations have not flourished. Another factor that appears to limit the recovery of moose populations when deer are not present is their ‘social carrying capacity’ (Bontaites and Gustafson 1993). In urbanized areas, moose begin to pose a real or perceived threat to human life and property and increasingly become victims of collisions with cars and trains (Karns 1997).

9.2.3 White-Tailed Deer (*Odocoileus virginianus*)

White-tailed deer are among the animals in New England forests most used by humans during the last 5,000 years. Their hides were shipped to Europe in a vibrant commercial trade that peaked around 1700 (McCabe and McCabe 1984).

Although it is difficult to imagine given today's overabundance of deer in suburban and rural areas alike, deer were overhunted to near extirpation in all but the unsettled portions of the ecoregion by the late 1800s. In some places, concerns for white-tailed deer populations prompted the closure of hunting seasons in Massachusetts as early as 1698 (Bernardos et al. 2004). Throughout the 1800s, the combined influence of market hunting and deforestation acted to depress white-tailed deer populations to a fraction of their original abundance (Miller et al. 2003). In the U.S., available funding stimulated by the passage of the Pittman-Robertson Wildlife Restoration Act of 1937 enabled organized restoration efforts to begin in the late 1930s with almost immediate success (Miller et al. 2003).

White-tailed deer have experienced shifts in their distribution in response to changes in the regional climate and habitat conditions. The recent history of deer in Northern New York serves as a fascinating illustration of the ebbs and flows of deer populations in the region (Jenkins 2004). Deer were common throughout the Adirondack Mountains in the middle of the twentieth century – a time when the region was dominated by young forests with excellent winter browse and large predators had mostly disappeared. Numerous hunt clubs within the Adirondack Mountains were created with deer as the principal quarry. The designation of wilderness areas in the 1970s commenced a trend of aging forests. This, in concert with several winters in a row in the 1970s where snow was exceptionally deep, triggered sharp reductions of deer populations in the region. Currently, deer are more common outside the Adirondack Park than within, promoted by the widespread abandonment of farms and decreasing numbers of hunters since the 1950s. In New Brunswick, white-tailed deer were actually absent when settlers first arrived, but archaeological evidence from middens indicated that they did reside in the region before the onset of long and cold winters and deep snows. Deer eventually reached New Brunswick again during the period of moderating climate following the Little Ice Age (Parker 2004).

White-tailed deer are one of the most successful North American mammals in modern times, with populations readily thriving in conditions created by human settlement. Overabundance of white-tailed deer is in fact a challenging issue for wildlife managers from the perspectives of both human conflict and ecosystem health (Warren 1997). Regarding the latter, overbrowsing by deer populations have well-documented cascading impacts on forest ecosystems (Côté et al. 2004). Along with the decline of hunting (Bernardos et al. 2004), the cultural perspective of deer 'is undergoing a remarkable shift in recent decades from a noble and wild game animal to neighborhood pest' (Foster 2002).

The most important limiting factor for white-tailed deer, determining the northern extent of its distribution at any given time, is snow accumulation in winter, which can increase mortality (de Vos 1964). White-tailed deer also require an abundant supply of relative young hardwood trees and shrubs and, therefore, tend to be absent from older-aged forests. In contrast to historical times, the average deer today is in minimal danger of being shot and killed other than at certain times of the year, especially close to human settlement. Deer populations have responded favorably to year-round subsidization of food sources in agricultural fields and

suburban gardens and population densities reflect this, particularly in the absence of predators. Strongholds of white-tailed deer across the Northern Appalachians are almost a mirror image of that of moose, although zones of overlap are increasing. Overall population numbers are probably quite close to pre-exploitation levels, speaking to the propensity of this species to rebound from population lows under the right conditions (McCabe and McCabe 1984).

9.2.4 *Wolf (Canis lupus or lycaon)*

At one time widespread across North America and Eurasia, wolves persist in just a fraction of their historic global range today. Their story in the Northern Appalachians is one of abundance at the time of European colonization followed by sharp declines, with little sign of recovery at present. Owing to their generalist habitat tendencies, wolves were at one time widespread throughout the ecoregion. Population declines were largely driven by direct persecution, chiefly aided by the bounty system. The first wolf bounty in the region was established by the colony of Massachusetts in 1630 while the last wolf in the state was shot 200 years later (Bernardos et al. 2004). Wolves stood in the way of the new life of European settlers who had become accustomed to keeping free-ranging hogs and sheep in their predator-free lives back home (Conover 2002; Whitney 1994). While direct persecution was responsible for most mortalities, changes in land cover and declining prey levels likely dealt the final blow (Foster 2002). Wolves disappeared from Nova Scotia by 1845–1847 (Scott and Hebda 2004), the Adirondack Mountains by the mid-1890s (Kays and Daniels 2009), Northern New England by the early 1900s (Whitney 1994), and New Brunswick by the early 1920s (Lohr and Ballard 1996).

In contrast to Northern Appalachians where wolf populations have never rebounded, the process of wolf recovery in the Western U.S. began in the 1970s under the umbrella of the Endangered Species Act to considerable success. Not only did the species begin receiving protection from exploitation and farming, but sources of conflict with domestic animals declined at the same time as ungulate prey populations in the region increased. Recovery in the Great Lakes and the U.S. Rockies was kick-started by a handful of active reintroductions and aided by the natural expansion of Canadian wolves (Paquet and Carbyn 2003).

Today, wolves are traditionally regarded as synonymous with western notions of wilderness. As one of the most maligned animals in human history, however, the principal limiting factor for their occurrence has not been habitat disturbance but rather direct persecution. In human-dominated landscapes, road density offers an excellent proxy for this threat (Mladenoff et al. 1995). However, roads fail to predict wolf presence in environments where human settlements and agriculture do not prevail (e.g., areas with forestry) and thus where encounters with humans and conflict with livestock are infrequent (Musiani and Paquet 2004). Judging by the successful expansion and reintroductions elsewhere in North America, wolves have an inherent ability, by virtue of their exceptional adaptability and favorable life-history

traits (Weaver et al. 1996), to withstand high levels of mortality and rebuild following population declines when provided the opportunity.

Potential habitat for wolf populations in the Northern Appalachian/Acadian ecoregion have been identified in several independent analyses (Carroll 2003; Harrison and Chapin 1998; Paquet et al. 1999) with all authors commenting that the likelihood that members of Ontario or Québec populations would arrive into the region on their own accord is seriously limited by human barriers (Wydeven et al. 1998). Nevertheless, in 2002, one canid confirmed through genetic analyses to be an ‘eastern wolf’ was trapped in the eastern townships of southern Québec (Villemure and Jolicoeur 2004). While no crossing of the St. Lawrence River has ever been documented, wolves, particularly subadults, can be highly mobile, and elsewhere they have colonized previously occupied habitat decades after their extirpation (Gehring and Potter 2005). The extent to which neighboring populations in Québec can serve as a source for population recovery in the Northern Appalachians is likely to be highly limited, given the high levels of hunting and trapping pressures outside reserves in the St. Lawrence Valley (Carroll 2003), not to mention the open-water barrier of the river itself, which is an active, year-round shipping channel with 4-lane highways and associated human settlement that parallel the river (Harrison and Chapin 1998).

A complicating factor in re-constructing historical distributional trends of the wolf in Eastern North America is the taxonomic confusion characterizing this species. A prevailing hypothesis is that wolves currently residing in Eastern Canada belong to *C. lycaon* – a species distinct from northern timber wolves (*C. lupus*; Wilson et al. 2003). However, since the eastward spread of coyotes, interbreeding is common between wolves and coyotes, such that large canids inhabiting the region today are actually hybrids of several forms (Kyle et al. 2006; Leonard and Wayne 2008). Jenkins (2004) has most aptly described wolves and coyotes as ‘end-points of a genetic continuum.’ Still unclear is which wolf species occupied the ecoregion historically where they are now absent (Forbes et al. in press). With the smaller *C. lycaon* being primarily a predator of white-tailed deer, it is an open question as to what predators exploited once abundant moose, caribou, and elk populations.

9.2.5 Coyote (*Canis latrans*)

The most successful colonizing mammal in recent history, coyotes were not present in the Northern Appalachian/Acadian ecoregion in historical times (Parker 1995; Forbes et al. in press). At the time of European settlement in the Western U.S. (ca. 1830), coyotes were limited in their distribution to the prairies and grasslands of the midwestern portion of the continent. Beginning in the early 1900s, they expanded rapidly eastward through both natural means and casual transplantations (Parker 1995; Voigt and Berg 1987). Coyotes first penetrated Ontario in 1919, colonized New York in the 1950s, reached the south shore of the St. Lawrence River in 1963, and arrived in Newfoundland in the 1990s (Fener et al. 2005; Larivière and Crête 1992; Parker 1995). They were firmly established in the ecoregion by the 1980s (Parker 1995).

From a mammalian perspective, the speed of their colonization in the East was unusually swift: in Maine, it proceeded at a rate of 1,867 km²/year and in New York, at 2,240 km²/year (Richens and Hugie 1974).

Prior to the twentieth century, coyotes did not venture far from grassland habitats (Voigt and Berg 1987). Their eastward expansion coincided with landscape alteration through intensive logging and agricultural development and the local extermination of gray wolves – a chief competitor in forested habitats (Larivière and Crête 1992; Parker 1995). At the same time, improved habitat conditions for white-tailed deer, together with a more favorable climate and the disappearance of wolf, facilitated coyote range expansion northward (Parker 1995). Bounties were immediately set up upon first discovery of coyotes in Maine in the early 1930s ‘to concentrate efforts towards their extermination’ (Aldous 1939). However, efforts to control coyotes in this manner throughout their North American range have been largely ineffective (Bekoff and Gese 2003).

Coyotes occupy a great range of habitats but are not as abundant in dense forest as in more open or disturbed habitats (Kays et al. 2008). Similar to white-tailed deer, the range of the coyote appears to be limited by snow cover and food resources. The disappearance of the wolf in the ecoregion not only paved the way for the entrance of coyotes but enabled it to secure a spot as the top terrestrial predator in the region (Gompper 2002). Having grown larger in size than their grassland progenitors and evolved into efficient predators of deer, they appear to serve as a partial ecological replacement for wolves in the ecoregion (Ballard et al. 1999). Coyotes do not coexist well with wolves; studies have documented direct and indirect competition with larger carnivores, involving outright killing and other behavioral shifts (Bekoff and Gese 2003).

9.2.6 *Black Bear (Ursus americanus)*

At one time occurring in all forested habitats across North America, black bears lost substantial portions of the southern part of their original range in the 1800s through the twin threats of overexploitation and habitat loss. Together with white-tailed deer, they have been the most used among large mammals in the Northeastern North America during the past 5,000 years and the most common food animal in Indian middens (Loskiel 1794, cited in Whitney 1994). Black bears were hunted to near expiration in the nineteenth century. Along with wolves, they were subject to bounties in Northeastern North America upon the arrival of European settlers, and other indiscriminate hunting in defense of people, livestock, and crops (Parker 2004). Once this pressure relaxed in the age of conservation and management, and forest cover returned in Northeastern North America, the conditions for black bear population growth were reinstated (Foster 2002). Populations began recovering virtually without interruption everywhere in the range where human settlement and accompanying road densities were not too intense (Pelton et al. 1999).

Currently, black bears can be found in most forested regions away from heavily settled areas in the ecoregion. In areas with substantial human development, black

bear habitat has become increasingly fragmented or has disappeared. For example, clearing of forest for agriculture and human settlement along the St. Lawrence River between Montreal and Québec City, forest clearing through human development in Central New Brunswick, and suburbanization in Southern New England has led to loss of black bear habitat even as populations were recovering elsewhere in the region. They were extirpated from Prince Edward Island by 1937 and have not reclaimed this range (Williamson 2002). Most black bear mortalities are human-related, through hunting, poaching (for a limited global trade in bear body parts), killing of nuisance bears, and vehicle accidents (Williamson 2002).

Black bear populations are thought to be stable in the Northern Appalachian/Acadian ecoregion and are even increasing in some areas (Pelton et al. 1999; Williamson 2002). Like with wolves, the life-history traits of black bears – age of first reproduction, life span, and litter size – bestow populations of this species with an ability to recover quickly from declines. Black bears are not necessarily limited by human disturbance and are able to adapt within short time periods to human settlement (Beckmann and Berger 2003). However, large home range sizes of bears mean that road crossings are generally inevitable, which become more frequent, with associated higher mortality risk, with increased density of the road network (Brody and Pelton 1989).

With the simultaneous expansion of human and bear populations, these two species have come into increasing contact in recent decades. In such cases of coexistence, the documented sightings and incidents of ‘nuisance bears’ have been growing, with individuals (particularly subadult males and females) increasingly engaged in crop and livestock depredation, apiary damage, and garbage raiding. Their propensity for this behavior increases in years when failures in berry production during drought periods necessitate wide-ranging searches for alternative food sources. Indeed, bears are readily attracted to year-round predictable food sources in areas of human settlement, and the physical movement of populations from wildlands has been followed by shifts in behavior, morphology, and ecology of black bears (Beckmann and Berger 2003). As such, over the course of the past century, the mandate of wildlife management departments throughout the region has transferred from black bear harvest control and population restoration to management of human conflict (Hristienko and McDonald 2007). The prevailing strategy by jurisdictions is to kill or relocate nuisance individuals and rely on areas that are protected from human intrusion to maintain populations (Mattson 1990). Under such conditions, when individual bears can become habituated to humans, their increasing visibility to humans can trigger perceptions that overall bear populations are thriving or even overabundant. In fact, however, increases in mortality due to such conflicts and the draining of populations from wildland areas can have the opposite results (Beckmann et al. 2008).

9.2.7 *Wolverine (Gulo gulo)*

As a circumpolar species, wolverines are largely confined to boreal and tundra regions of North America, thriving most in landscapes that have been largely

unaltered by humans (Copeland and Whitman 2003). This is another species that has lost a large part of its original range, although the extent of this loss is not well-understood due to incomplete knowledge of its historical distribution (Aubry et al. 2007). However, the wolverine is commonly identified as an extirpated species in the Northern Appalachians (e.g., Bernardos et al. 2004; Foster et al. 2002) and on state and provincial endangered species lists (Table 9.1). Yet it is unknown the extent to which southern historical records reflect extreme dispersal events and occurrences that are in fact extra-limital (Copeland and Whitman 2003). Once researchers finally made a concerted effort to assemble and verify historical observation records, the conclusion for the Northeastern U.S. was that wolverine occurrence was, at best, 'sparse and haphazard' (Aubry et al. 2007). Of the 11 wolverine records that extended down to Pennsylvania since the early 1800s, only two, both from New Hampshire, were considered verifiable. The latest one was from 1811 (Aubry et al. 2007). Either wolverines disappeared prior to that time or they were never very abundant. No parallel verification effort has been conducted for the Eastern Canadian provinces. Wolverines are assumed to have occurred historically in Québec south of the St. Lawrence River and Northwestern New Brunswick (Slough 2007; Wrigley 1967 in Forbes et al. in press) but it is unknown whether such records have been verified. The species never occurred in Nova Scotia or Prince Edward Island (Scott and Hebda 2004; Slough 2007). de Vos (1964) identified their distribution in the neighboring Great Lakes region as widespread but 'nowhere common.' The northern stronghold of the species has in fact receded or disappeared from Québec and Ontario, with fewer possibilities for dispersing individuals to find their way north of the St. Lawrence River (COSEWIC, 2003; Dawson 2000).

Currently confined to northern environments, wolverine distribution in North America is closely associated with persistence of snow cover through the spring denning period (May–June; Aubry et al. 2007). Such conditions no longer exist in the Northern Appalachian/Acadian ecoregion except at the highest elevations and are expected to disappear altogether under most scenarios of climate change (Chap. 15). Like many larger-bodied carnivores, protection from overexploitation and the availability of large-ungulate prey biomass serve as additional requirements for this species. Wolverines are identified in the popular imagination as creatures of wilderness, although whether humans have caused the retreat of wolverines into such areas or their required conditions are simply confined to areas where human development has not yet extended is still an open question. As noted by Copeland and Whitman (2003), however, 'large tracts of pristine habitat may be the only assurance of their continued existence.'

9.2.8 *Cougar (Puma concolor)*

Cougars, or mountain lions, were at one time the most widely distributed animal in the New World, after humans, occurring in forested habitats all the way to the

Table 9.1 Explanatory factors driving relative abundance and distributional dynamics of large mammal species in Eastern North America

Species	Human landscape change	Climate limitations	Directly interacting species	Official status
Caribou	Mature coniferous forests critical; tolerate low levels of disturbance	Northern, deep snow	White-tailed deer (disease transmission), wolves, coyotes, bears (predators)	COSEWIC (CA): end NB: ext; NS: ext; QC: thr
Moose	Favor early successional forests; upper limit of settlement and road density	Northern, temperature	White-tailed deer (disease transmission)	NS: end
White-tailed deer	Thrive in early successional forests, agricultural and suburban edges	Southern, limited by deep snow, cold winters	Wolves, coyotes, bears (localized predation)	–
Wolf	Generalist habitat associations; upper limit of road density and settlement dictated by human conflict	No climate limitations	–	ESA (US): thrNS: ext; ME: sc; NH: end; NY: ext
Coyote	Generalist habitat associations;	Southern, limited by deep snow, cold winters	Wolves (competitor/predator)	–
Black bear	Favor early successional forests; upper limit of road density and settlement	No climate limitations	–	–
Wolverine	Low tolerance for human conflict	Northern, require deep spring snow for denning	Wolves (competitor)	NB: ext; QC: end

(continued)

Table 9.1 (continued)

Species	Human landscape change	Climate limitations	Directly interacting species	Official status
Cougar	Generalist habitat associations; upper limit of road density and settlement dictated by human conflict	No climate limitations	–	ESA (US): endNB: ext; VT: end; NY: ext
Canada lynx	–	Morphologically adapted for deep snow	Bobcat (competitor)	ESA (US): thrNS: end; NB: end; ME: SC; NH: end; VT: end; NY: thr
Bobcat	–	Limited by deep snow	Lynx (competitor)	QC: SC

Note that overexploitation is a potential significant driver for all species. See individual species accounts for references. Status codes: end, endangered; thr, threatened; SC, special concern; ext, extirpated. Categories are defined and assessed at the jurisdictional level

southern tip of South America (Young and Goldman 1946). In Northeastern North America, the range of this carnivore likely extended as far north as that of white-tailed deer, with a northern limit of Southern Québec (south of the St. Lawrence River), Central Maine, and Northern New Hampshire (Parker 1998). They were most common in the rugged portions of the ecoregion, such as the Adirondack, Green, and White Mountains. As with other large carnivores, the eighteenth and nineteenth centuries brought about rampant persecution and targeted bounties. The consequence was widespread loss of range and population declines on the continent. In Vermont, for example, the bounty on cougars was one of the first acts instated in the very first session of the legislature, and was not discontinued until 1904 (Parker 1998). Bounty records and those from the famous 'circle hunts' provide some evidence that cougars were captured in large numbers until the early decades of the nineteenth century and continued to appear in the records until the late 1800s (Parker 1998). When combined with large-scale habitat loss and depletion of large ungulate prey in the Northern Appalachians, cougars were considered to be extirpated from the entire ecoregion by the late 1800s, having disappeared from strongholds to the south, such as Massachusetts and Connecticut even earlier that century. Goodwin (1936) claimed the Adirondack Mountains to be the final stronghold of cougar in Eastern U.S., last recorded in New York in 1894. However, Brocke (2009) contended that the mountain ranges and surrounding areas of the Adirondacks were never rugged or vast enough to support populations of this wide-ranging carnivore and that the false impression of their abundance was generated by fraudulent bounty collections.

Cougar have lost as much as two-thirds of their historical range in North America (Pierce and Bleich 2003); the process of natural recovery since the 1960s has been aided by active protection measures, evolving human attitudes, and increasing ungulate populations. Moreover, pockets in the West largely devoid of human influence acted as source populations for range expansion, which has occurred to a modest extent in Midwestern U.S. and Canada through subadult dispersal (Nielsen et al. 2006). The cessation of active hunting of cougars and the resurgence of forest cover in Northeastern North America has not, however, resulted in the recovery of cougars, as it has in the case of other large mammals such as black bear and moose. The most likely reason is that source populations of extant cougars in Western North America are separated at too far distances over highly settled, and therefore inhospitable, terrain.

No animal in the ecoregion sparks as much passionate debate regarding its continued existence. Indeed, the controversy has steadily heightened since the 1980s with hundreds of sightings reported in Northeastern North America (Jenkins 2004; Stocck 1995). Logs of such sightings and other evidence such as tracks and hairs are kept faithfully in most jurisdictions or by independent enterprises, but few are verifiable. Confirmed records verified and collated by The Cougar Network, for example, indicate that the preponderance of these in North America are located in the vicinity of the contiguous western range of this species, with only a smattering in the Northern Appalachians (The Cougar Network 2009; Nielsen et al. 2006). In New Brunswick and Québec, several hair and track samples collected since 2002 have

been confirmed through DNA analyses to belong to cougar, and in 1996 a cougar was killed by a truck in the Eastern Townships region of Estrie, Québec, not far from the New Hampshire border (Forbes et al. *in press*). Of seven samples, three are of South or Central American origin, indicating that these individuals are escaped or released animals or the offspring of once captive animals. DNA analysis on the other four samples could not reject a similar identity (Forbes et al. *in press*).

This chapter does not seek to resolve this mystery, and the pursuit of evidence of the existence of the ‘eastern’ cougar will undoubtedly continue unabated. Even if definitive conclusions about the existence and origin of this species in the ecoregion cannot be made at this time, it is safe to say that the species exists nowhere near the densities approaching the ecological functional role that it plays in western environments or that it supposedly did in historical times in this part of the world. Whether what is currently present represents the seeds of a future population remains to be seen and should be closely monitored. It should also be noted that where populations of cougars are established in Western North America, their presence is readily confirmable through roadkills, incidental take through trapping and hunting, and track surveys (Kurta et al. 2007; Parker 1998).

Cougars are catholic in their habitat requirements, with prey availability, vegetation structure, and topography determining habitat use (Pierce and Bleich 2003). Human fear and conflict were the root causes of cougar extirpation in the ecoregion, and while this may not translate into the same likelihood of mortality, the potential for conflict still exists. In suburban areas where they have been studied, cougars are known to navigate through remaining natural areas, adjust their activity patterns, and for the most part move about unnoticed (Beier 1995). While individuals from established populations tend to avoid roads and associated human development, they can be less discerning when traveling short distances through inhospitable terrain (Beier 1995; Logan and Sweanor 2001).

9.2.9 *Canada lynx (Lynx canadensis)*

Because early lynx records are impossible to distinguish from bobcat (Hoving et al. 2003), it is not possible to determine the relative abundance of lynx when European settlers arrived. What is known about the conditions of the Little Ice Age, however, suggests a favorable environment for this northern species. It is known that the southern range of Canada lynx once extended as far south as Connecticut and Pennsylvania, but has receded during the past century (Hoving et al. 2003). This species was also extirpated from Prince Edward Island in the early 1800s and mainland Nova Scotia by the 1920s (Parker 2001). Lynx are currently restricted to Cape Breton Island, Northwestern New Brunswick, the Gaspé Peninsula, and Central and Northern Maine (Hoving et al. 2003; Ray et al. 2002). Sightings continue to be reported from high elevation areas in Vermont and New Hampshire where suitable, albeit fragmented, habitat conditions occur (Ray et al. 2002). Jenkins (2004) referred to the Adirondack Mountains as ‘borderline lynx country at best.’ While reliable historical records do exist, whether they

represent occasional wanderers or residents has never been properly resolved. An unsuccessful reintroduction attempt in the Adirondacks took place from 1989 to 1991, with high mortality rates through vehicle collisions (Brocke 2009) and no evidence that the species resides in the area today (Weaver 1999). Certainly, the lack of continuous expanses of coniferous-dominated forests coupled with a less-than-robust snowshoe hare (*Lepus americanus*) population would preclude this possibility (Jenkins 2004).

The main reduction in lynx range in the ecoregion occurred around the turn of the twentieth century; the species was no longer detected in Southern Maine after 1904. Records of lynx in this part of the world were essentially absent for the first half of the 1900s and then began to increase steadily after 1973 (Hoving et al. 2003). Unlike wolverine, once researchers began to scour historical observation records, it became clear that lynx do enjoy a population stronghold in Northeastern North America, contrary to previous impressions of the species being primarily confined to the western part of the continent currently and in the past (e.g., McKelvey et al. 2000).

Lynx are primarily restricted to boreal forest habitats, which in the Northern Appalachian/Acadian ecoregion extend southward only into cool and mesic high-elevation areas (Hoving et al. 2005). They are particularly limited by the availability of snowshoe hare, their preferred prey throughout their distribution. Habitat conditions for lynx in the southern periphery of its range tends to be highly variable in distribution and quality, where hares do not tend to achieve the same peak abundances as they do in northern boreal forests (Murray et al. 2008). The Québec portion of the Northern Appalachians contains the most robust lynx populations and likely serves as a source for the rest of the ecoregion (Ray et al. 2002). Genetic analyses have confirmed the relative isolation of Northern Appalachian lynx from populations that occur north of the St. Lawrence River, which is unlikely to be well-connected due to tremendous development activity alongside the river and year-round open waters due to shipping (USFWS, 2000).

The southern distribution of lynx appears to be limited by deep snow conditions (Hoving et al. 2005), which confer the lynx with a competitive advantage over bobcat and other potential competitors such as coyote (Parker et al. 1983). This notion is supported by (1) the expansion of bobcat range following the contraction of lynx range in the early 1900s (de Vos 1964; Hoving et al. 2003; Lariviere and Walton 1997); (2) the recent incidence of naturally occurring hybridization between bobcats and lynx at the southern edge of lynx range in Maine, New Brunswick, and Minnesota (Homyack et al. 2008); (3) the retraction of lynx range corresponding with changes in climate in the region, including recent warming trends with less snowfall (Hoving et al. 2003); and (4) reduction in lynx range in Southern Alberta associated with the interactive effect of roads and coyotes (Bayne et al. 2008).

9.2.10 Bobcat (*Lynx rufus*)

Bobcats are currently the most widely distributed among North American native felids (Anderson and Lovallo 2003). This situation, however, has been by no means

static over the past two centuries, with the Northern Appalachian/Acadian ecoregion a case in point. Further confusing the historical record is the fact that bobcat and lynx were not distinguished in the literature with any consistency until the mid 1800s (Hoving et al. 2003). Some evidence suggests that bobcats were not very abundant when the early European colonists arrived but that they benefitted from early land clearing associated with human settlement (Litvaitis et al. 2006). There were bounty programs within bobcat range beginning in the early 1800s, but records did not generally differentiate lynx and bobcat (Litvaitis et al. 2006). Beginning in the early 1900s, a northward expansion of the distribution of this species took place concomitant with land clearing for agriculture, ameliorating climate and snow conditions following the end of the Little Ice Age, and a corresponding northward retreat of the southern limit of lynx (de Vos 1964; Hoving et al. 2003; Lariviere and Walton 1997; Litvaitis et al. 2006). Throughout the first half of the twentieth century, bobcat records began to appear in localities where they were hitherto unknown (e.g., Cape Breton [Parker et al. 1983] and Southern Maine [Hoving et al. 2003]).

Although bobcats have never been present on Prince Edward Island, the current distribution of this species extends across the rest of the ecoregion. In the past four decades, however, its upward trend appears to have reversed somewhat; population declines have provoked the listing of this species in some jurisdictions (Litvaitis et al. 2006; Table 9.1). Its broad distribution belies this felid's specialist tendencies as an early successional habitat 'obligate' (Litvaitis 2001); population declines have been associated with overall decline of such habitats in the region (Litvaitis 2003). Furthermore, because bobcat declines occurred at the same time that coyotes began to secure their foothold in the region, some authors have suggested a competitive relationship between the two species (Brocke 2009; Hoving et al. 2003; Litvaitis and Harrison 1989). On the other hand, bobcats have continued to move into areas formerly occupied by lynx (Hoving et al. 2003), and hybridization between the two species has been recorded at this frontier (Homyack et al. 2008). Snow depth plays a likely role in limiting the northern range of bobcats (Hoving et al. 2003; McCord 1974). They are not morphologically adapted for travel in deep snow, and their winter habitat use appears to be governed by avoidance of such conditions. As a result, they are inferior competitors with lynx in areas characterized by severe winters (McCord 1974). Some areas of prime habitat have been consistently occupied by bobcats for four centuries (Litvaitis et al. 2006). Where bobcat populations occur at modest levels, their persistence is further challenged by high road densities and otherwise modified landscapes, incurring heightened levels of mortality (Litvaitis et al. 2006).

9.3 Learning from the Past to Plan for the Future

Wildlife populations and hence communities have been highly dynamic in Northeastern North America over the past 300 years (Bernardos et al. 2004; Foster et al. 2002; Whitney 1994), as illustrated by the patterns of the ten large mammals

discussed here (Fig. 9.1). Most of these species have experienced relatively dramatic declines and recoveries in their relative abundances and distributional shifts in the region since colonization by European settlers. The trajectory of each species has been unique, affirming the tendency of responses to the changing ecosystem context to be highly species-specific. Relative abundance and distributional limits reflect a legacy of species-specific habitat associations, sensitivities to human disturbance, levels of conflict with human residents, and adaptations to climate (Table 9.1).

The exhibited patterns do, however, fall into four general categories that represent distinct trends in dynamics characteristic of large mammals in Northeastern North America (modified from Foster et al. 2002; Bernardos et al. 2004):

1. Species declining historically with recent increases and recovery: moose, white-tailed deer, and black bear
2. Species declining historically with little or no recovery: wolf, wolverine, caribou, cougar, and lynx
3. Species expanding their range: coyote
4. Species increasing with forest clearance and agriculture and decreasing with forest maturation: bobcat and white-tailed deer

Inherent in shifting ecological conditions over the past 400 years has been the changing role of the human footprint (Cronon 1983; Fuller et al. 2004; Whitney 1994). The history of land-use change in the Northern Appalachian/Acadian

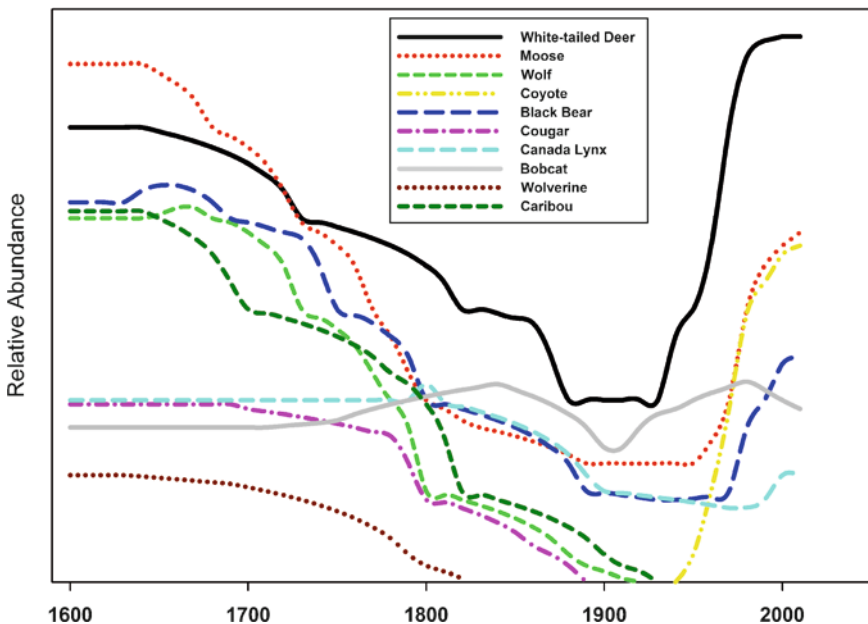


Fig. 9.1 Historical trends of ten large mammal species profiled in this chapter. Each species is represented by a generalized pattern averaged over the ecoregion; local dynamics are not captured

ecoregion has taken place in several discrete stages and provides the background behind the faunal changes discussed here. From the time of arrival of European colonists in the late fifteenth century, the region was dominated by an agrarian economy where individual pursuits of survival and subsistence dominated land use patterns. Industrial growth commenced in the late 1700s, accompanied by the transportation revolution, which signaled the emergence of canals, road networks, and railways. Of relevance to wildlife, market hunting was facilitated by this development, in addition to the invention of the repeating rifle and the refrigerated railroad car. As such, this period was defined by peak levels of exploitation, through hunting and trapping, of the region's fauna and the first extirpations and even extinctions. All this coincided with the highest levels of land conversion from logging and human settlement during the latter half of the nineteenth century. It was at this time that the opening of the American West began to promote a geographic shift of commercial-scale agriculture in that direction. Accordingly, widespread cropland abandonment commenced in 1860s in Eastern North America, setting the scene for the gradual re-growth of forest cover from a virtually denuded state at that time.

The turn of the twentieth century also brought in a new era of conservation and management that allowed many populations of large mammals to climb from historic lows. While forest cover in the region has by now returned almost to its earlier extent of coverage, land uses of the past have been supplanted by extensive suburbanization, increasing industrialization, and fragmentation of natural areas (Woolmer et al. 2008). This character of disturbance presents an altogether novel challenge for biological diversity: full conversion from natural vegetation to human infrastructure for dwelling and transportation purposes, resulting in long-term or permanent habitat loss with little chance for successional recovery (Fuller et al. 2004; McKinney 2006).

Ensuring that planning and regulatory tools provide adequately for the persistence of biological diversity requires a comprehensive understanding of the factors that threaten the conservation of individual species. Centuries of changing circumstances provide a good opportunity to gain understanding of the relative vulnerability of large mammals to threatening processes – information that is vital for effective conservation planning (Wilson et al. 2005).

With habitat loss being the overwhelming cause of species endangerment in modern times (Sala et al. 2000), it is natural to view this as the dominant historical driver of species population and distributional dynamics in Northeastern North America, given the known changes in land use that have occurred. However, over-harvest, climatic conditions, species interactions, and societal attitudes have also played important roles. The interacting and cumulative nature of all four factors, in addition to time lags in ecological response (Bernardos et al. 2004), complicate our ability to understand the strength of the role of each driver.

First, although the reasons differed according to the species, all 10 large mammals were subject to uncontrolled killing, an activity that began as soon as the first settlers arrived (Cronon 1983). As a corollary, concerted efforts to manage populations in the form of harvest control and some augmentation promoted the gradual recovery of many, although not all, these species beginning in the 1900s (Conover 2002).

Second, climate conditions also underwent broad-scale shifts during the same period. The Little Ice Age between the 1300s and mid-1800s was characterized by unusually cold temperatures, with the coldest temperatures in Northeastern North America recorded in 1776 (Fagan 2000). A gradual warming trend occurred in the region through the 1800s.

Third, direct and indirect interactions with sympatric species through killing, predation risk, or competition can be key determinants of wildlife abundance and distribution patterns on the landscape (Ritchie and Johnson 2009). Range shifts for both Canada lynx and bobcat have occurred in opposite patterns from one another over the past century, likely reflecting a competitive relationship interacting with snow depth (Krohn et al. 2004). Coyotes would likely never have been so successful in invading the region without the preceding demise of wolf populations and may likewise have influenced present-day patterns of bobcat distribution and abundance (Brocke 2009). Predation can also play a limiting role for ungulates in particular, although this is most likely to occur in localized situations on small populations (Ray et al. 2005).

Finally, social attitudes governing individual human behavior as it relates to coexisting with ungulates and carnivores have also undergone substantial shifts in this region. Broadly speaking, the historical ‘shoot-on-sight’ philosophy held by every settler who feared for his life or livelihood or needed food on the table has palpably changed to today’s level of tolerance by comparison (Conover 2002). This means that direct mortality at the hands of human co-inhabitants has declined. This has, of course, been aided by the fact that most of the large predators, particularly wolves, are no longer present. People in the Northern Appalachians are less likely to be relying on a subsistence existence, so conflicts are less deleterious to overall livelihoods, and the wildlife management policies (including some control programs) are now in place to address conflicts (people may be more apt to call an official to address a conflict rather than deal with the situation themselves). Many of the species discussed here that survived last century’s era of exploitation have also become, at least to some extent, ‘culturally conditioned,’ having developed strategies to co-exist amid human infrastructure, and displaying a flexibility in their behavior and ecology (e.g., Beckmann and Berger 2003). Nevertheless, current increases in development and low-density housing patterns are bringing about heightened opportunities for conflicts; for example, suburban and exurban developments (Kretser et al. 2008) can increase population mortality rates (Beckmann and Berger 2003).

9.4 Planning for Ecoregional Conservation Through the Lens of Large Mammals

The discipline of conservation planning has emerged as a systematic process to plan for biological diversity conservation in response to its continued loss in the face of an expanding human footprint (Groves 2003; Margules and Pressey 2000). In the Northern Appalachian/Acadian ecoregion in particular, the need to ensure that the remaining natural areas and native biological diversity are protected and

adequate management measures at the human–wildlife interface are in place against the backdrop of a continually changing environment has led to the mounting imperative for comprehensive conservation planning at multiple scales (Trombulak et al. 2008).

Species should figure prominently in such exercises both as targets of conservation interventions but also as tools to guide conservation area design (Groves 2003; Ray 2005a). It stands to reason that large mammals in particular, by virtue of their life history requirements, vulnerability to certain threatening processes, and cultural connections (both negative and positive), should be of particular use in this regard. For example, such species may be useful for informing both the goals and broader vision of a conservation planning exercise. They may also be used to define high-level aspects of a conservation ‘blueprint’ itself. When it comes to real-world implementation, however, using a surrogate or focal species approach to guide land-use planning decisions is fraught with challenges (Favreau et al. 2006). The most formidable among these are that (1) the cost and length of time required to collect suitable data on such species to guide decision-making is often in conflict with budgets and timeframes for decision-making, and (2) the extent to which chosen species can fulfill any promise to serve as adequate surrogates for myriad other components of biological diversity is often too readily assumed and seldom tested. Understanding the promises and limitations of the role of large mammals in such exercises, therefore, is paramount for effective conservation planning. In the discussion that follows, I will address both of these in concert by outlining both the manner in which large mammals can play useful roles in conservation planning and the limitations of such an approach.

9.4.1 Large Mammals as Conservation Targets

At the root of any conservation planning exercise is the vision that drives it and a set of goals or targets that describe its ultimate purpose. Desired outcomes often include biological diversity targets, or those set for individual species (Groves 2003; Tear et al. 2005). These can represent a desire either to maintain or restore the status of individual species (or even their elimination in the case of exotics). Planners must make decisions about two particular aspects of their stated objectives as they relate to large mammals. The first is which species to focus on, and the second is the state of the target, spelled out in qualitative or quantitative terms, to be addressed in conservation planning (Chap. 17).

A list of species that serve as conservation targets in a planning exercise will include those on federal, provincial, or state species-at-risk lists or other extinction-prone species, recognizing that focused attention is likely required to ensure their recovery. Others will be selected as targets under the assumption that attention to their conservation will bring about benefits for numerous co-occurring species (Groves 2003; Ray 2005a; Sanderson 2006). Large mammals of the Northern Appalachians serve as examples of both categories.

Inherent in choosing species that will receive special attention are decisions about restoration targets that have always occupied the ambitions of some of the more visionary conservationists in the region. Whether restoration is envisioned through active reintroduction attempts or through more passive means of natural recovery (as may currently be true for cougars and is certainly true for moose), room must be made for such species in the planning context. Otherwise, if ever-changing circumstances, such as an expanding human footprint or warming climate, compromise overall habitat quality and leave little room for space-demanding animals, formulating plans for their reintroduction is simply irresponsible. Success is unlikely if the same factors that drove the disappearance of such creatures are left undiminished. The failed introductions of Canada lynx and caribou in the region demonstrated some of these pitfalls. With the science of reintroductions having increased markedly in sophistication since then (Seddon et al. 2007), such misjudgments are less likely to occur in the future.

The oft-cited desire to restore the full complement of large mammals that were present when colonists first arrived must be tempered by reality, including the increasingly unfavorable climatic and associated habitat conditions in the ecoregion for northern species like caribou and wolverine. By contrast, the ambition to restore wolves in the region has stimulated multiple serious analyses of the ecological potential of such an enterprise, indicating that the notion is not so far-fetched (Carroll 2003; Harrison and Chapin 1998; Paquet et al. 1999; Wydeven et al. 1998). During the time it takes geneticists and ecologists to sort out what taxonomic form of wolf is truly native to the region (Rutledge et al. 2009), it is possible that they will make their way into the ecoregion from populations to the north and west and establish themselves on their own. Finally, it must be stated that while accounting for the restorative potential of large mammals in conservation planning allows for the expression of ambitious dreams and rallying points for optimism, the trade-offs in terms of time, energy, and resources must be evaluated.

The second decision relevant to conservation planning concerns the state of species targets, or the specific desired outcomes. The key role of population size and trend as a determinant of vertebrate extinction risk (O'Grady et al. 2004) underscores the importance of this step. The ultimate planning objective for a species should at the very least strive for demographic sustainability of identified populations, but it can be as ambitious as achieving historic population levels or ecological functionality or as modest as merely ensuring the presence of the species (Sanderson 2006). Our ability to predict the capacity of the Northern Appalachian/Acadian ecoregion to support large mammal densities makes accurate 'reference levels' for resident wildlife populations challenging: few would have predicted even 20 years ago that moose populations would achieve the heights they have in some areas of the region or how rapidly coyotes would colonize new areas. Likewise, the more effort that has been put into radio-collaring and surveying Canada lynx in Maine, the higher the population estimates rise. Minimum viable population estimates are readily attainable (Sanderson 2006), as are general rules of thumb for population levels (7,000 adults; Reed et al. 2003). One challenge is the difficulty of evaluating population boundaries for wide-ranging species without demographic or genetic

data or unless they are isolated (e.g., Gaspé caribou), or alternatively, assessing the amount and quality of habitat that is required to support viable populations. The more heterogeneous the habitat or the broader the scale of planning, the more difficult it will be to set and measure progress against specific population-level targets.

An attractive option is to set historical ‘baseline’ conditions as population-level targets. The many changes that have characterized the ecoregion, however, render this a somewhat futile exercise (Motzkin and Foster 2004). It is difficult enough to ascertain which species were present at what time in the past or even the population levels of species in the region today. It is also not possible to establish what represents the true baseline conditions or those within the ‘natural range of variability’ (Landres et al. 1999). For example, conservationists are often wooed by the historical accounts of large-mammal abundances when the settlers first landed in Northeastern North America, but it is difficult to know the extent to which erstwhile perceptions of such great quantities were merely influenced by their comparisons with the relative impoverishment of large mammals back home, or even whether predator populations here became artificially high in response to the abundance of livestock animals that reached the shores at the same time (Anderson 2004). Against this backdrop, current cultural constraints and extent of permanent conversion of the natural landscape may be the ultimate determinant of population-level targets.

9.4.2 Large Mammals as Conservation Tools

While much has been written about the validity of assumptions that underlie the role of focal species in conservation planning (e.g., Favreau et al. 2006; Ray 2005a), the following discussion centers on the manner in which large mammals can be of use in this particular geography. In Western North America, where mammal communities are represented by a diverse array of large-bodied ungulates and carnivores, their role in conservation planning can more easily be justified (Carroll et al. 2001; Noss et al. 2002). In the Northern Appalachian/Acadian ecoregion where human settlement prevails, the community is somewhat a relic of the past, with the species most sensitive to prevailing threats having disappeared. Those that remain are for the most part habitat generalists that exhibit sometimes remarkable degrees of flexibility and adaptability to the human-dominated landscape. So how can large mammals in this landscape aid us in conservation planning? Keeping in mind not only that large mammals must be joined by other species to make a full complement of focal species (Coppolillo et al. 2004), or that many other conservation tools than use of focal species exist (Groves 2003; Tear et al. 2005; Trombulak et al. 2008), large mammals can serve as guides for several elements of conservation plans, including the location of core conservation areas and priorities for connectivity, ecological thresholds of development, and management options outside conservation areas.

Core Areas With body size directly related to home range size (Lindstedt et al. 1986), large mammals are generally among the most space-demanding representatives of regional biological diversity. Accordingly, they should be of use in guiding the extent and selection of conservation areas, or those that are designated as off-limits to major development and associated roads. For most large mammals considered here, past and present strongholds are the relatively unsettled areas of the ecoregion at the far end of the continuum of human impact. This statement may appear contradictory from a local perspective since many large mammals in this region exhibit surprising abilities to adapt to the human landscape. Nevertheless, the importance of such areas to population persistence of most such species is quite clear when viewed from a broad scale. It is highly probable, for example, that the recovery of black bear and moose in the region would not have been possible without the persistence of these wildlands, although this is difficult to quantify. As has been demonstrated with black bear elsewhere, at the same time individuals driven by an opportunistic and curious nature have been attracted to anthropogenic food sources, the high-enough mortality they suffer renders such areas population sinks (Beckmann and Lackey 2008). Species such as cougar apparently have been limited in their ability to recover in this area as they have in the West due to the long distances from source populations.

Developing recommendations for the size of such wildland patches is risky since those who implement such guidelines have a tendency to regard these as minimum sizes. In addition, none of the species under discussion here requires wilderness areas to the exclusion of the anthropogenic landscape, making it that much more difficult to develop recommendations for required size of core areas. Clearly, accommodating the needs of large mammals generally requires areas of natural habitat several orders of magnitude above those required to meet those of bird, plant, or invertebrate communities (ELI, 2003). Because minimum areas can be calculated in a variety of ways (e.g., occupancy analyses, species-area relationships, and minimum viable population estimates), it is easy to be confused by scientifically-derived recommendations.

Ultimately, the landscape context in which such fragments are embedded has as much or more importance than the size of the patches themselves in contributing to persistence of large mammals (Franklin and Lindenmayer 2009). Designing landscapes to minimize fragmentation and maximize overall extent of natural cover over scales that are meaningful for populations may have more dividends than a focus on securing large patches which, if embedded in hostile landscapes, may be relatively worthless (Ray 2005b). Specifically, minimum patch size will be less important than the overall amount and dispersion of habitat and the intensity of the human footprint in the intervening landscape. Cookbook remedies or rules of thumb regarding size of core areas to receive protection are therefore generally inappropriate (Ray 2005b).

At present in the Northern Appalachians/Acadia ecoregion, a number of sizeable blocks of core unroaded area serve undetermined functions for the persistence of large mammals. Depending on the scale of planning, one option is to build targets for individual fragment sizes around calculations for the area needed to support a

certain number of individuals of carnivore or ungulate, or alternatively, identify those that are too small to be able to reliably contribute to mammalian conservation (e.g., Kerley et al. 2003). Another is to identify source areas through spatially explicit population modeling (Carroll 2007) or grid-based landscape population modeling (Fahrig 2001) and keep such areas as intact as possible. Even in the absence of precise formulation of minimum areas required, the scale and ambition of a planning exercise will be ratcheted up a notch or two if the continued viability or recovery of wide-ranging species like black bear, wolves, moose, Canada lynx, and bobcat is accommodated.

Connectivity Designing for connectivity between natural areas is also a critical feature of conservation planning for large mammals as well as other species (Hilty et al. 2006; Chap. 16). Connectivity is a species-specific and scale-dependent emergent property of landscapes, facilitating movement of organisms across heterogeneous landscapes (Schmiegelow 2007). It enhances the value of, but cannot replace, the role of core areas (Noss and Daly 2006). Connectivity becomes an issue for these animals in landscapes that have undergone extensive development where pinch points that impede species movements begin appearing. Providing for connectivity becomes imperative to prevent the isolation of populations or subpopulations. For example, moose habitat on mainland Nova Scotia is already isolated, which is one assumed driver of their population decline and genetic impoverishment in this area (Beazley et al. 2006).

Given the sometimes extensive movements of large mammals, accommodating their needs in this regard can be another way to scale up the ambition of a conservation plan. However, although the concept of corridor placement in land-use planning is generally widely embraced, in practice, the objectives of the corridor are often disconnected from the manner in which animals actually move through the landscape (Chetkiewicz et al. 2006). It is not always possible to view the relative permeability of a fragmented landscape through our own eyes, yet most corridors are designed on the basis of how humans define connectivity. As such, it is vital to distinguish structural connectivity with functional connectivity from the viewpoint of individual species (Hilty et al. 2006; Chap. 16). Identifying habitats suitable for linking core areas should be based on knowledge of the species' response to vegetation, land use, road density, and topography (Beier et al. 2006) and to behavioral decisions regarding individual movements (Chetkiewicz et al. 2006).

The species-specific nature of planning for linkages becomes most important in landscapes where multiple options for connectivity still exist. Otherwise, 'path of least resistance' approaches will be easiest to spot in circumstances where these are vanishing, and it is a matter of saving what is left before it vanishes (Noss and Daly 2006). Ideally, the latter approach would be accompanied by careful monitoring of selected species to understand their movement decisions in such a context and to evaluate the effectiveness of designed linkages. We should, however, be careful to remind ourselves of the habitat generalist nature of many of the remaining large mammals considered here. Because many can and do move through marginal and degraded habitats, a corridor designed for any of them does not serve most habitat specialists with limited mobility (Noss and Daly 2006). Nevertheless, ensuring that

conservation designs accommodate the long-range movements of large mammals that have high dispersal requirements and for which some anthropogenic environments, such as roads, constitute barriers will add value and ambition to planning at various scales. The more modified the landscape and the more connectivity is compromised, the more important this step becomes, as long as such species remain residents.

Thresholds of Landscape Change Large mammals should serve as a useful lens to tackle questions of conservation design from yet a different direction. Rather than wring our hands over ‘how much is enough,’ we can ask ‘how much is too much?’ In other words, we can draw from the science investigating impacts of land-use change on wildlife populations to guide conservation planning efforts that place limits on the extent and intensity of our human footprint (Schmiegelow et al. 2008). This obviously depends on the extent to which land-use changes represent threatening processes to a particular species and whether an empirically-derived relationship is known or can be evaluated between population status and degree of habitat loss, fragmentation, or degradation. While most of the species profiled in this chapter are not habitat specialists and enjoy wide distributions when not overharvested, the reviews provided here demonstrate that all show some upper limit of human development that can be tolerated lying somewhere on the continuum between unroaded wilderness and a parking lot (Table 9.1).

The science of ‘thresholds’ is in its relative infancy and again will generally be both species- and context-specific. One rich area relevant for this discussion is the evolving field of road ecology. A recent review of the population-level effects of roads and traffic on animals confirmed that for large mammals, the impacts are predominantly negative (Fahrig and Rytwinski 2009). Most affected are those species that have large movement ranges and do not avoid roads or traffic and for which increased mortality leads to population declines because of low reproductive rates (Forman et al. 2003). Species like cougar, black bear, and wolf appear to be absent from areas with relatively high road densities where they occur, either because of behavioral avoidance or increased mortality (Dickson and Beier 2002; Fahrig and Rytwinski 2009; Mladenoff et al. 1995; Morrison et al. 2007). For wolves, multiple studies have even identified road-density thresholds beyond which wolves have a high probability of extirpation in settled landscape (Fuller et al. 1992; Mladenoff et al. 1995; Wydeven et al. 2001). Similarly, bobcats in New Hampshire do not appear to occupy potential home ranges with more than one major road (Litvaitis et al. 2006). For some species in this region, such as moose, high road densities may not have particularly deleterious impacts on population size, but may nevertheless limit the extent to which populations will increase or expand their range.

Because roads are an integral part of the human footprint in that the building of human infrastructure is always accompanied by roads, this is a fruitful area on which to focus planning efforts. In this regard, rather than planning for roads in a piecemeal fashion, conservation design would contain some notion of an upper limit to road density before build-out occurs. Future scenarios of road development can occur in a predictable fashion, particularly as it relates to exurban settlement (Baldwin et al. 2007). Combining this insight with knowledge of road density

thresholds for large mammals would add a refreshingly proactive dimension to land-use planning.

Thresholds of overall habitat conversion and extent of fragmentation may provide additional guidance for conservation planning (With and Crist 1995). However, the relationship between such parameters and the occurrence or population status of large mammals has not been explored to the extent it has with other species (e.g., birds [Radford et al. 2005; Trollope et al. 2009]; American marten [*Martes americana*; Hargis et al. 1999]). Context, particularly scale, will likely complicate our ability to generate rules of thumb for this as it relates to large mammals. Hence, concentrating on core area for design purposes would, for the time being at least, constitute a more prudent approach.

9.4.3 Other Considerations for Using Large Mammals in Conservation Planning

When large mammals are among the residents of a landscape, conservation planning must incorporate several additional factors that transcend traditional conservation design. While not necessarily unique to this wildlife group, three factors – planning for change, management measures, and monitoring – must be integral to any conservation plan that explicitly considers this group of species.

Planning for Change Most conservation designs are inherently static entities. Patterns of biological diversity and the processes that generate them, including human threats, tend to be evaluated for one point in time yet serve as the basis of plans for which the goal is to maintain diversity in the future. It is, however, increasingly clear that, to be effective, plans must take inevitable ecological changes into account. This includes not only natural processes that influence patterns of biological diversity, but the cumulative effects of human modification of landscapes and a rapidly changing climate (Pressey et al. 2007; Chap. 15).

While thresholds of tolerance to modified landscapes will probably remain the same for a given large mammal species, the locations and size of core conservation areas and key linkages almost certainly will not. Accordingly, designs that designate core areas but particularly those that aim to maximize connectivity must provide for anticipated range shifts in response to changing conditions in addition to movements within home ranges or dispersal among populations (Noss and Daly 2006). Emerging analyses that predict future habitat conversion (e.g., Baldwin et al. 2007, 2009; Trombulak et al. 2008) and ecological consequences of a changing climate (Rodenhouse et al. 2009) should be used to forecast future scenarios of landscape condition. These can in turn be related to the status of large mammals (e.g., Canada lynx; [Carroll 2007]) to make necessary adjustments to elements of conservation design that have a better chance of accommodating future change and the considerable uncertainty associated with it.

Management Measures to Mitigate Impacts on Large Mammals No matter how robust a conservation design, some degree of management intervention above

and beyond the conservation plan will be required to better ensure large mammal populations are conserved. Wildlife management includes active interventions beyond land-use designations that range from habitat manipulation, to harvest regulations, to mitigation strategies for development infrastructure (e.g., roads), to strategies aimed at dealing with nuisance animals, including culling of populations. Because protected areas are not likely to surpass a mere fraction of most ecoregions, management practices in the intervening ‘matrix’ habitats outside such areas are required to help ensure that these do not become hostile environments and instead actively contribute to the conservation landscape as a whole (Franklin and Lindenmayer 2009).

This review makes clear that the changing status of all 10 profiled large mammals has occurred against a backdrop of shifting human attitudes (Conover 2002). Indeed, particularly when it comes to large carnivores, only adjustments in human behavior will enable some wildlife populations to achieve some level of security. This factor will only increase in importance the more human populations encroach on wildlife habitat, as with low-density exurban sprawl (Kretser et al. 2008). In light of the reality that many present-day large predator populations do not likely exist at densities that allow for an expression of their functional ecological roles, special strategies must be devised that not only seek to replace or augment the role of such animals (e.g., in highly settled areas) but foster a wider expression of acceptance for their continued presence.

Monitoring A third obligatory feature of conservation planning relates to long-term monitoring of the status of large mammal populations. This is important for testing how they are faring in response to land-use designations or management interventions that have been put in place for their welfare. Monitoring the effectiveness of such activities is unfortunately often among the first line items to be removed from budgets during periods of financial restraint but is critical for achieving adequate understanding of how interventions ultimately relate to large mammal conservation status. While many strategies detailed in this chapter have been devised in the name of conserving large mammals, it is rare for them to come with demonstrated success since prescriptions are seldom accompanied by long-term monitoring information.

Budgetary limitations are not the sole challenge that stands in the way of this. The life-history characteristics of the animals discussed here (large-bodied, long-lived, wide-ranging, and often elusive) mean that designing robust survey protocols over sufficiently large areas that will have the statistical power to be able to detect true trends over time is logistically challenging, to say the least (MacKay et al. 2008). Arguably for many species, present-day techniques render this unfeasible. Responses of large-mammal populations to both management and changing ecological conditions are difficult to determine either because of confounding and interacting factors or because of the reality of time lags in response. Nevertheless, a commitment to monitor large-mammal populations will not only help to inform the success of conservation planning in that landscape (as long as management responses are nimble enough to change course in response to the weight of evidence), but those with similar conditions elsewhere.

9.5 Lessons Learned

In this chapter, I have pieced together existing information on the individual trajectories of 10 large mammal species over the past four centuries of change in the Northern Appalachian/Acadian ecoregion. Several broad categories of patterns emerge: species that have declined historically with recent increases and recovery, those that have declined historically with little or no recovery, those that have expanded their range into the ecoregion in recent history, and those already resident in the area that have fared particularly well with forest clearance and expanding agriculture but have then decreased in localized areas with forest maturation. Nevertheless, the path of each individual carnivore and ungulate species has been unique, demonstrating the interplay between background conditions and the particular inherent characteristics of each. Because the past has been defined by alternate periods of decline and recovery of environmental conditions, it has provided an interesting perspective on the interactions between drivers such as land-use change, climate shifts, prevailing human attitudes, and interspecific relationships. In any case, this exploration underscores the reality that in any given place in the ecoregion the large-mammal community structure (as defined by the relative abundances of component species) has undergone significant shifts over this time period.

This retrospective analysis has some clear usefulness for ongoing and future land-use planning, in that it has provided insight into both the limitations and conservation prospects of individual species, many of which serve as conservation focal points, by virtue of their high-profile status. As such, these species can be important not merely as targets of conservation activities in their own right, but can effectively serve as planning tools. This can be as simple as expanding the scale of ambition for conservation by wrapping their fates in the success of the plan, but also as a means by which to guide the identification of core conservation lands, connectivity within the overall landscape, and thresholds of development intensity.

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