CHAPTER 7

Wildlife Dynamics in the Changing New England Landscape

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Although the forest dynamics that we have examined were profound and characterized by major shifts in land cover and forest composition, they occurred gradually within the time frame of daily life and off in the woods, where they have been easily ignored by much of the general population. The same cannot be said of the remarkable changes that have occurred recently in the wildlife of New England and much of the eastern United States (Figure 7.1). Over the past decade, nearly daily articles in newspapers and magazines have highlighted the ongoing transformation in our animal populations and the management and health issues that accompany these changes. Many larger mammals and birds that have been uncommon for decades or centuries, such as bears, beavers, fishers, moose, eagles, turkeys, herons, and vultures, are increasing and are regularly encountered in backyards, along roadsides, or in fleeting views; whereas many familiar and cherished bird species of agrarian landscapes, including bobolinks, meadowlarks, woodcock, whippoorwills, and openland sparrows, are declining or have disappeared locally (Figure 7.2). Meanwhile, species that have never inhabited the region have immigrated, in some cases across great distances, or have been introduced and are increasing in density, visibility, and ecological importance.

With these changes, wildlife managers, conservationists, and many citizens are confronted with major policy issues and ethical dilemmas. What changes are really occurring? Should we attempt to maintain populations of declining species, and if so, how? How do we control, manage, and live with the growing numbers of larger species? More fundamentally, what social, biological, or environmental factors underlie and explain these changes? A historical perspective may assist in educating and even modifying the behavior of the human population that interacts with this dynamic wildlife. In a region with immense tracts of maturing forestland, but a growing and largely suburban population, the range of issues involving wildlife extends from the desire on the part of many

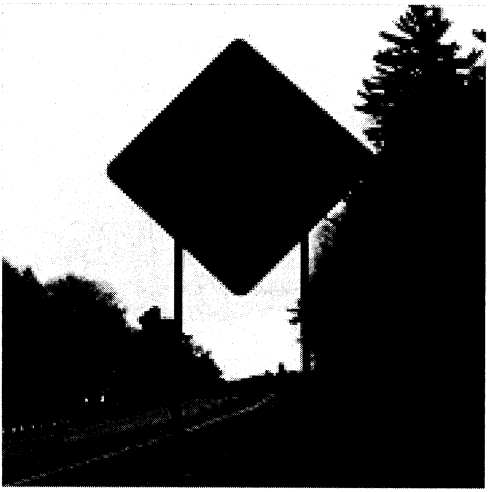
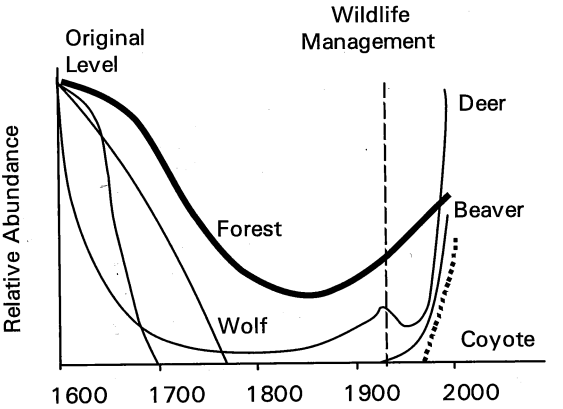


Figure 7.1. A moose-crossing sign along a Massachusetts highway highlights the dynamic and increasingly wild nature of the land. In the 1850s Henry Thoreau noted that the largest wild animal in the landscape was the muskrat. Photograph by D. R. Foster.

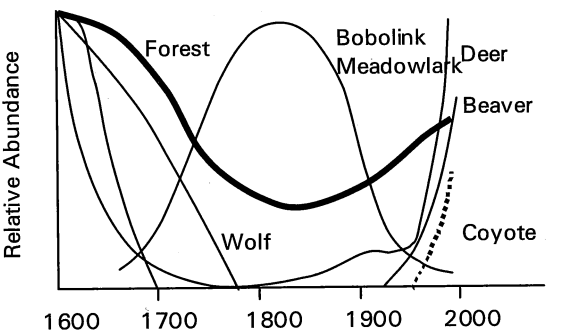
conservationists to restore large carnivores such as wolves and cougars, to an appreciation for wildlife by the general population, balanced with concerns for human safety and personal property that appear to be posed by a handful of species.

To address these ecological questions and management issues, there is a critical need for long-term data along with a historical perspective similar to that which we have used to evaluate and discuss forest dynamics. Such an approach to these issues also offers an opportunity to answer basic ecological questions about the factors controlling wildlife populations, the nature of the feedbacks that exist between plant and animal species, and the contrasts between the dynamics of wildlife and plant assemblages.

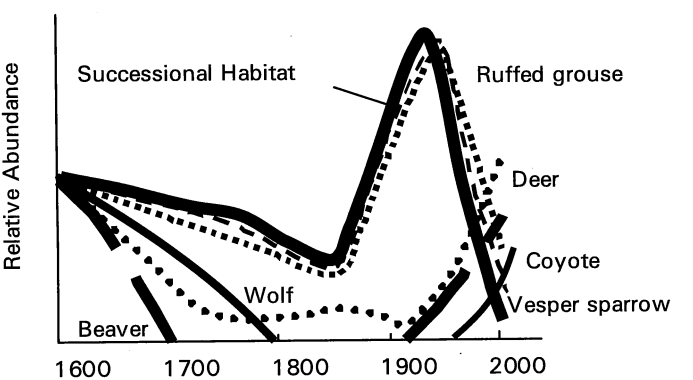
In pursuit of a long-term perspective on wildlife dynamics, we collected historical data on animal populations for southern New England and analyzed these in order to do the following: (1) document the major trends in wildlife populations since European settlement; (2) identify the loss or arrival of major species and resulting changes in wildlife assemblages; (3) relate these dynamics to changes in the physical, biological, and cultural environments; (4) integrate this information with our historical perspectives on vegetation dynamics in order to increase our understanding of forest processes through time; and (5) provide a context and background for interpreting current changes in order to guide policy for management and conservation.



a. Bickford and Dymon (1990)



b. O'Keefe and Foster (1998; modified from Bickford and Dymon, 1990)



c. DeGraaf and Yamasaki (2001; modified from Bickford and Dymon, 1990)

Approaches and Methods

The spatial scale, time frame, and species that we investigated were selected through a process that blended ecological and management interests with pragmatism. The compilation of records extending over hundreds of years requires identification of a common geographical reference area—something akin to a common denominator for data. Although many sources of wildlife data exist, most records are grouped by political unit, with state governments and agencies providing the most comprehensive recent information and town records and histories, aggregated to a state level, providing critical information for the early colonial period. In consideration of these factors, we opted for taking a statewide perspective, which offers the advantages of considerable data and ample variation in such factors as environment, vegetation, and land use. As data sources vary considerably from one state to the next, we limited our analysis to a single state—Massachusetts. From an ecological perspective this provides a good context for our other studies. Moreover, Massachusetts incorporates a wide range of the environmental and cultural gradients that are broadly representative of New England and that provide for diversity in habitat and wildlife dynamics. Finally, since much of the legislation and policy concerning wildlife originates at a state level, these data are relevant to major societal needs.

Data Sources

We utilized a variety of sources and incorporated the resulting information into our statewide GIS and database. Unfortunately, and rather surprisingly, there are no Massachusetts-wide data from archaeological studies that would provide an overview of pre-European faunal use and distribution. Consequently, though we used some archaeological sources, our earliest records focus on explorers' accounts, town and state legislation, bounty and harvest records, natural histories, scientific studies, museum collections, newspaper and other popular accounts,

Figure 7.2. Three related but different graphs interpreting major historical wildlife trends in Massachusetts. Panels a and b suggest that the landscape was heavily forested at the time of European settlement. Panel b (O'Keefe and Foster 1998b) is adapted from panel a (Bickford and Dymon 1990) but does not emphasize the role of management in the recovery and dynamics of species. It also includes openland bird species to underscore the fact that many species thrived and increased in the nineteenth-century agricultural landscape and subsequently declined with reforestation. Although panel c (DeGraaf and Yamasaki 2001) is also modified from panel a, it interprets the pre-European landscape as extensively covered with successional habitat due to Indian activity and natural disturbance and suggests that openland species were abundant at the time of European settlement. Modified from Foster, Motzkin et al. 2002.

and town and county histories. Although varying in taxonomic detail, data density, and accuracy, these sources provide a strong qualitative to semiqualitative picture of changing wildlife populations and help to identify some of the factors driving these changes. In particular, histories of the more than 300 towns in the state, mostly written between the mid-1800s and mid-1900s, provide a wealth of information, frequently including species lists, bounty records, anecdotal descriptions of changing wildlife populations, and dates of last and first observations. The large number of towns in the state allows us to overcome the spatial and temporal gaps in individual records and to develop fairly robust interpretations of changes through time.

In addition to town histories, many scientific studies provide overviews of the ecology, behavior, and status of individual animal species. Many also contain summaries of historical trends for particular species over time. Meanwhile, twentieth-century information on population estimates, harvests, accidental deaths (for instance, roadkills), sightings, and management activities is maintained by the Massachusetts Division of Fisheries and Wildlife in their annual reports, Game Population Trend and Harvest Surveys, and unpublished records.

Species Examined

In our melding of ecological and management interests with pragmatic constraints, we focused on species that are important to the function of forested and other natural landscapes, represent particular social and conservation concerns, and are fairly consistently represented in available records (Table 7.1). These criteria also satisfied one of our original objectives, namely, to use the history of wildlife and the New England landscape to convey a strong sense of ecological dynamics to the broad public. Thus, our data are necessarily biased toward game species, larger birds, persecuted "vermin" species, and selected animals of conservation focus. In contrast, most songbirds, amphibians, reptiles, fish, small mammals, and invertebrates are largely excluded from our analysis because they are incompletely represented in historical data and documents.

Cultural and Environmental Setting for Interpreting Wildlife Dynamics

Previous chapters provide detailed information on the climatic, vegetation, and human history of New England. Consequently, we need to expand on these only with information particularly relevant to wildlife populations. Relatively few detailed data exist on the status of wildlife for the Late Woodland period before the first European settlers. Nonetheless, it is important to underscore our earlier observations that

Table 7.1. Historical Dynamics of Birds and Mammals in Massachusetts and Adjoining Areas of New England

Regionally Extirpated or Extinct (+)

Bicknell's thrush	Eastern gray wolf	Sea mink (+)
Great auk (+)	Elk	Wolverine
Heath hen (+)	Indiana bat	Woodland bison
Labrador duck (+)	Lynx	Woodland caribou
Loggerhead shrike	Marten	
Passenger pigeon (+)	Mountain lion	

Openland and Successional Habitat (species generally declining)

Northern harrier	Brown thrasher	Upland sandpiper
Northern bobwhite	Nashville warbler	Vesper sparrow
Killdeer	Chestnut-sided warbler	Savannah sparrow
Spotted sandpiper	Prairie warbler	Grasshopper sparrow
American woodcock	Yellow-breasted chat	Bobolink
Mourning dove	Eastern towhee	Eastern meadowlark
Common nighthawk	American tree sparrow	Black-throated blue warbler
Whippoorwill	Field sparrow	Mourning warbler
Least flycatcher	Indigo bunting	
Horned lark	Red-winged blackbird	New England cottontail
Purple martin	Veery	Red fox
Bank swallow	Golden-winged warbler	Woodchuck
Barn swallow	Brown-headed cowbird	
Sedge wren	Baltimore oriole	
Ruffed grouse	Magnolia warbler	
Eastern phoebe		
Eastern bluebird		

Introduced Species (*introduction failed)

Cattle egret	Black-tailed jackrabbit	Black rat*
Mute swan	European hare*	House mouse
European starling	European rabbit	
House finch	Eastern cottontail	
House sparrow	Norway rat	
Ring-necked pheasant		
Northern bobwhite		
Rock dove		
Wild turkey (reintroduced)		

Range Expansion

Northward or eastward

Little blue heron	Northern rough-winged swallow	Golden-winged warbler
Glossy ibis	Tufted titmouse	Nashville warbler
Turkey vulture	Carolina wren	Worm-eating warbler
Black vulture	Blue-gray gnatcatcher	Northern waterthrush
Mourning dove	Northern mockingbird	Louisiana waterthrush
Barn owl	Blue-winged warbler	Northern cardinal
Red-bellied woodpecker	Cerulean warbler	
Acadian flycatcher		Virginia opossum
		Coyote

Southward

Herring gull	Bohemian waxwing	Rusty blackbird
Great black-backed gull	Magnolia warbler	Purple finch
Golden-crowned kinglet	Swamp sparrow	
Hermit thrush	White-throated sparrow	

(*continued*)

Table 7.1. Continued

Historically Continuous Species		
Downy woodpecker	Common yellowthroat	Gray squirrel
Eastern wood pewee	Song sparrow	Mink
Eastern kingbird	Common grackle	Muskrat
Gray catbird	American crow	Porcupine
American robin		Raccoon
Yellow-rumped warbler	Bobcat	Red squirrel
Ovenbird	Eastern chipmunk	
Recently Increasing Species		
Woodland species		
Wood duck	Tree swallow	Beaver
Hooded merganser	Brown creeper	Black bear
Northern goshawk	Wood thrush	Fisher
Red-tailed hawk	Worm-eating warbler	Gray fox
Broad-winged hawk	Scarlet tanager	Moose
Blue-headed vireo	Red-headed woodpecker	White-tailed deer
Great horned owl	Wood duck	
Barred owl		
Pileated woodpecker		
Others		
Great blue heron	River otter	
Snowy egret		
Great egret		
Canada goose		
Mallard		
House wren		
Evening grosbeak		

Source: Modified from Foster, Motzkin et al. 2002 and compiled from DeGraaf and Yamasaki 2001, Massachusetts Department of Fisheries, Wildlife and Environmental Law Enforcement, and other sources.

the landscape was dynamic and to note that human influences on animal populations certainly predated the establishment of Plymouth Plantation in 1620. Archaeological studies clearly indicate that Native American populations were strongly dependent on a diverse array of animals from terrestrial, freshwater, and marine ecosystems. Humans undoubtedly influenced the abundance and population dynamics of many of the upland species that we will consider, either directly through hunting and trapping or indirectly through habitat modification by fire and clearing for villages and encampments. Indeed, the extreme view, refined and revisited many times over the past four decades, by Paul Martin at the University of Arizona, and recently championed by many authors, is that the aboriginal Americans strongly shaped the composition and abundance of at least large game animals over the past 12,000 years across the Americas.

The very earliest Europeans to arrive in the region, the explorers, trappers, settlers, and traders, had such an immediate major effect on the land, the Indian population, and individual animal species that

most of our early historical descriptions depict a time when New England's wildlife was already very much in transition. As European explorers traveled the coast and progressively made their way inland, they carried diseases and took animal furs to ship back to Europe. As epidemics decimated Indian populations and altered their social structure, wildlife must have been affected indirectly through changes in hunting pressure and rapid alteration of wildlife habitat around local settlement areas. Trapping had a more direct, though highly selective impact; European trading with Indians led to a rapid and widespread decline in beaver, lynx, and other valuable furbearers across the New England states. Consequently, the early colonial landscape that we routinely think of as a baseline for historical studies was actually changing on a yearly basis.

The details of historical land use had an uneven effect across Massachusetts, for example, varying considerably with distance from the coast; from major urban centers like Boston, Worcester, and Springfield; and from agricultural centers like the Connecticut River Valley. Clearing proceeded most rapidly and extensively along the coast and in the Eastern Lowland and Connecticut River Valley, with the rougher Berkshires being settled last and supporting among the largest contiguous forest tracts in the nineteenth-century landscape. Surprisingly though, the greatest extent of forest persisted just south of Boston in the eastern part of the state at the base of Cape Cod, where extensive sandy outwash plains dissuaded settlement and agricultural clearing. Across the New England landscape, the treatment of nature was largely driven by utilitarian attitudes with only slight regard for limits in natural resources. This, plus the lack of a European hunting tradition among the general population, led to a widespread overutilization of fish, mammals, and birds as well as sustained efforts to eradicate "vermin" species. Accompanying the agrarian peak of the nineteenth century were increases in market hunting, trade in feathers for millinery uses, and collection of natural history specimens.

With agricultural abandonment, forests returned unevenly across the state, and mill towns and dams increased in number and size on major waterways. Agriculture persisted in the broad lowlands, and forests expanded most rapidly and completely in the western part of the state. The late nineteenth century brought new appreciation for wildlife, including conservation, fueled in part by the concern of Bostonian ladies for the birds slaughtered for the millinery trade and a new hunting ethic espoused by sportsmen's clubs. Professional wildlife management focused on game species and led to the creation of the Massachusetts Commission of Fish and Game in 1886; the onset of licensing, hunting, and fishing regulations; and a wide range of species introductions.

Through the twentieth century and into the twenty-first, Massachusetts became increasingly industrialized, suburbanized, and heteroge-

neous in human distribution, land cover, and wildlife habitat. In particular, today a greater proportion of the population lives in suburban areas. Differences in population density, agricultural land, and road networks across the state have increased immensely during the past century. The Berkshire Plateau and northern Worcester County remain relatively undeveloped and largely forested; eastern and southeastern Massachusetts from Boston and the South Shore toward Worcester are intensely fragmented by human activity; Cape Cod and the Islands are increasingly developed for summer homes and recreation; and the Connecticut River Valley juxtaposes farm fields, housing, and industry with wooded swamps and isolated forested mountains. Although the extent of forestland peaked in the past decade, forest age continues to increase as brushy grasslands, shrublands, and young woodlands are still being replaced by older forest. In addition, development, suburban fragmentation, and "parcelization" (progressive reduction of forest lot sizes) continues, particularly in eastern Massachusetts. Meanwhile, social attitudes toward wildlife and wildlife management and regulations have changed considerably in the past 100 years and are increasingly shifting from an emphasis on consumption to one of conservation and preservation.

General Trends in Wildlife Dynamics

Historical data for nearly 100 species highlight species-specific dynamics and long-term trends that are highly individualistic. Each of these histories can be broadly interpreted in relation to the species habitat preferences and land-cover changes, in the context of specific human pressures, especially hunting or trapping. However, despite these individualistic trends, generalization is possible. Six broad patterns are recognizable that capture the major temporal trends in wildlife dynamics (Figure 7.2b and Table 7.1).

A large group of species, including many large mammals and birds that were actively hunted and persecuted or that require extensive woodland habitat, exhibit a long-term historical pattern of decline and recovery. These species were widespread across the Commonwealth at the time of European settlement and then decreased rapidly and were either locally extirpated by the mid-nineteenth century or persisted in small, local populations. Over the past century and in distinctively individualistic patterns, they have increased, either rebounding naturally or with assistance from stocking and other forms of active management. In contrast, a group of open-land species was uncommon or absent at European settlement, increased greatly with agricultural clearing of forest to a peak in the nineteenth century, and has subsequently declined to oftentimes low abundance. This group includes many grassland, shrubland, and early-successional species that are the focus of modern

conservation efforts. Some of these species are common elsewhere; others are globally rare; and for many, records are inadequate to determine whether they are native to New England. A relatively small number of animals were extirpated from the state or region, including a few that became globally extinct. Although low in number, species in this group do include animals that were particularly important ecologically or that represent major cultural features of the New England landscapes. A number of bird species and at least two mammals have naturally expanded their ranges into Massachusetts from northern, southern, or western distributions. Nonnative species have been introduced purposefully or accidentally. In some cases these new species have become naturalized and quite abundant. Finally, numerous persistent species have fluctuated through hundreds of years of settlement but have not experienced the long-term directional changes in populations noted for other groups of species.

Species Declining Historically with Recent Increases and Recovery

This rebounding group is varied but predominantly composed of birds and moderate- to large-sized mammals that depend on and use forested environments. Many of these species are notable for their rapid recent increases and their high visibility to human residents. With many mammal populations currently increasing at 3 to 10 percent annually, this group is the focus of research and management as well as frequent human conflict.

Beaver *(Castor canadensis)* and white-tailed deer *(Odocoileus virginianus)* represent two of the numerous species that decreased early in the historical period and recently have increased substantially. These two are of particular interest because of the great influence that they exert on natural ecosystems and the significant management issues and concerns that they raise in the modern landscape (Figures 7.3 and 7.4). From archaeological, ethnographic, and historical sources, it is clear that both species were widespread, common, and important in pre-European forest ecosystems and Indian economies. Both were also important prey for large carnivores, including cougar and wolf. Beaver rapidly became a focus of trapping and trading for the French, Dutch, and English in the early seventeenth century, including John Smith, who returned to London in 1616 with 1,100 skins. In Massachusetts, revenue from the beaver trade helped to finance settlement activity and encouraged exploration. The shipment of pelts paid many of the expanding colony's debts to the homeland and gradually led to local extirpation of the species. As early as the early 1630s, Governor William Bradford reported shipments of more than 12,500 pounds of beaver pelts to England. The species was eliminated from southeastern Massa-

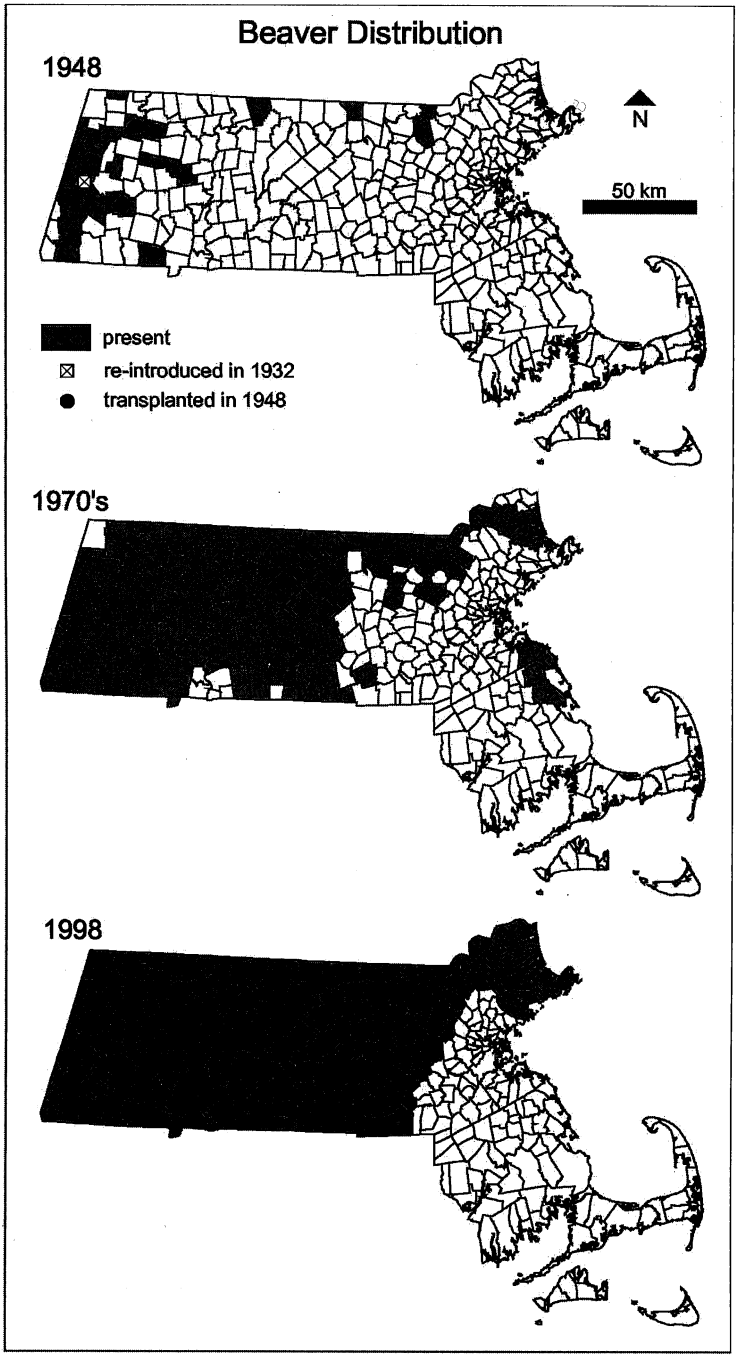


Figure 7.3. Modern expansion of the beaver population across Massachusetts following reintroductions in the 1930s and 1940s. The population in 2002 was estimated as exceeding 70,000 animals. Reprinted from Foster, Motzkin et al. 2002.

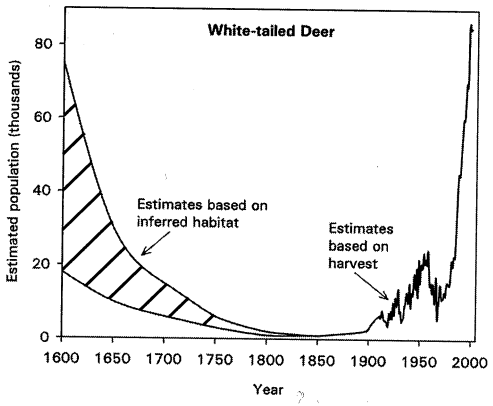


Figure 7.4. Historical changes in the population of white-tailed deer in Massachusetts. Two early scenarios are depicted that bracket the extreme high and low estimates at the time of European settlement. In the mid-nineteenth century small populations persisted in the Berkshire Hills in the west and near the base of Cape Cod in the southeast. Reprinted from Foster, Motzkin et al. 2002.

chusetts by 1635 and from most of the state, except the northern Berkshires, by 1700. As beaver were declining in southern New England, Indian and colonial trapping expanded to New York and Maine. The fur trade shifted to Canada by 1750, and beaver were completely extirpated from Massachusetts by the late 1700s.

After more than a century's absence, initial efforts were made to reintroduce beaver in the late 1920s, with the enactment of protective legislation and releases of New York beavers in western Massachusetts. Through the 1940s, numerous animals were relocated across the state, and with a population estimated at more than 300, a limited trapping season was established. The species expanded rapidly, both on its own and through continued relocation efforts on the part of state wildlife managers. By the late 1980s, the official assessment by the Division of Fisheries and Wildlife was that "beavers are deemed restored to all suitable habitats."

In the heavily wooded landscapes of central New England, with abundant streams, wetlands, and lakes, beaver are thriving, with a population recently estimated at 70,000. Increasingly, this relatively recent arrival is affecting forests by creating dams, which flood adjoining uplands, and selectively cutting trees and browsing other plant species. The ecological impact of beavers is difficult to overstate as they alter local hydrology and biogeochemistry, create wetlands, modify soils, flood and kill acres of forest, selectively alter vegetation composition, diversify landscape patterns, and create new habitats. The influence of these activities on other species is equally important. The ponds, open wet-

lands, dead trees, and forest openings created by beavers offer important habitats for many plants and animals in a landscape otherwise dominated by dense and continuous forests. The return and near omnipresence of beavers are major factors conveying the sense that New England is becoming wilder and more natural.

However, many effects of beaver, especially the raising of water tables and mortality of trees, have significant human consequences. Notably, the number of highway, housing, and septic system conflicts involving beavers has risen dramatically in recent years. In addition, beaver and other mammals may carry diseases such as giardiasis, a disease caused by the protozoan *Giardia lamblia,* which also causes human illness, and have the potential to spread them widely across the landscape. Despite the fact that most *Giardia* outbreaks in New England are probably of human origin (for example, from human waste fouling water supplies), beavers and other wildlife have been implicated in such outbreaks in a number of New England public water supplies, which has led to trapping, relocations, and heated public debate. In the absence of natural predators, beaver populations are continuing to expand and grow, and social conflicts are destined to increase. However, in a social environment inimical to trapping, a statewide referendum led to a ban on most leg-hold and body-gripping traps in Massachusetts in 1997. As a result, the number of animals trapped declined, from 1,136 in 1996 to 98 in 1998. With the beaver population continuing to increase and complaints to wildlife agencies continuing to rise, we face a major challenge as to how to live with or control this remarkable animal.

White-tailed deer underwent an analogous trajectory, although they were never completely eliminated from Massachusetts and did not require the same degree of active intervention to reach their current high density (Figure 7.4). Deer were important in both Indian and early colonial landscapes and economies. Deer remains are a consistent item in archaeological sites and generally constitute the most abundant vertebrate fossil. It is likely that Indians and the gray wolf were the species' major predator, as deer provided an important source of food, tool-making materials, and clothing. However, quantification of Indian impacts on deer, like population estimates for both species, is fraught with uncertainty. Heavy hunting by an expanding European population led to noticeable declines in the deer herd and the promulgation of many early, and ultimately futile, attempts at hunting regulation. In 1698, Massachusetts placed a closed season on deer between January 15 and July 15 and then enacted a three-year moratorium on deer hunting in 1718 when underenforcement of the original law and habitat loss led to further declines. Deer "reeves," one of the earliest attempts at game wardens in the United States, were appointed in each town in the Commonwealth in 1739.

Throughout the late eighteenth to late nineteenth centuries, deer became increasingly uncommon and were essentially extirpated from the central two-thirds of the state. A small population persisted in forested areas of Berkshire County in western Massachusetts and in the pine and oak woodlands in southeastern Massachusetts near the base of Cape Cod. A ten-year hunting moratorium starting in 1898, coupled with farm abandonment and a statewide increase in shrubland and woodland, produced the first rebound in the population, to an estimated 5,000 in 1905. The growing population led to crop losses, illegal hunting, and the establishment of a regulated hunting season by the Division of Fisheries and Wildlife. Although the season has been modified repeatedly in attempts to regulate the size and demography of the herd, the deer population has continued to expand, particularly since the 1940s. Currently, it is estimated at approximately 90,000 animals. On average, 10,000 deer are harvested by hunters annually, with another 7,000 killed by automobiles. However, hunting interest is declining across New England, and there are major questions concerning the potential to regulate the deer herd, especially in populated suburban areas, where hunting is often prohibited.

The expanding population of large herbivores affects forest ecosystems profoundly. Selective deer browsing alters the composition of tree seedlings, herbs, and shrubs and ultimately may have a strong and long-term impact on forest composition and structure. The sedentary behavior of deer, with adults seldom roaming more than three-quarters of a mile from their place of birth, may lead to significant local variation in effects. Landscape-level variation in deer browsing has been strikingly apparent in central Massachusetts. Active hunting throughout this broad area, including on Harvard Forest lands, has maintained a low deer population that has little effect on forest regeneration and composition. In contrast, a fifty-five-year ban on hunting in the nearby 60,000-acre Quabbin Reservation led to an extremely dense deer population and a severe understocking of seedlings, saplings, and understory trees. In many cases the forest had the open, fern-dominated appearance of a wood-pasture. Reinstitution of hunting at the Quabbin in 1991 was a controversial process that has succeeded in reducing deer densities and initiating a sustained pulse of understory recovery. Similar impacts, and management conflicts, abound across southern New England and much of the eastern United States, especially in suburban wooded areas where gardens are often the focus of impacts. The remarkable resurgence of the deer herd and the species' ability to thrive in areas heavily used by humans has been associated with unfortunate health consequences, notably the rapid spread of the tick-borne Lyme disease. As a consequence, the cultural perspective of deer is undergoing a remarkable shift in recent decades from noble and wild game animal to neighborhood pest.

Six highly conspicuous large birds are included in the group of rebounding species (the pileated woodpecker, wild turkey, raven, osprey, eagle, and great blue heron; other species undoubtedly increasing include raptors such as the great horned and barred owls). Pileated woodpeckers, the region's largest woodpecker species (approximately 30 centimeters tall), depend on large, standing dead trees for nesting sites. Although this species declined to low numbers as forests declined and remaining stands were intensively harvested, its population has expanded greatly with recent increases in forest age and maturity. Wild turkey, a forest-dwelling species, was widespread at the time of settlement and a common food for Native Americans and early European settlers. It was extirpated across the region by overhunting but was actively reintroduced in the 1930s. Turkey have increased across much of the state, reaching populations of 20,000 in 2002 because of the excellent habitat of open oak woodlands and agricultural land. The species is hunted extensively with bow, primitive firearms, and shotguns during the fall and spring seasons. The raven, which closely resembles the smaller crow, is a northern species that commonly feeds on carrion. This formerly uncommon species has expanded naturally back into southern New England as a consequence of increased food provided by rebounding wildlife populations and roadkill.

Osprey and eagle are large raptors whose populations were decimated by indiscriminate killing and antipathy toward raptors during the seventeenth, eighteenth, and nineteenth centuries. These species were further affected by shell-thinning caused by the bioaccumulation of the insecticide DDT. As a result of the banning of DDT, active establishment of nesting platforms, general improvement in water and wetland quality, the protection of coastal habitat, and change in public attitudes toward predators, ospreys are undergoing a remarkable rebound, from a low of less than fifty in the 1970s to more than 350 today. Although heavily concentrated in coastal areas, this species should continue to expand inland up the major riverways and into the watersheds of large lakes. Eagles have been reintroduced through active hacking programs and are expanding across New England. In Massachusetts, large winter populations congregate around the Connecticut River and Quabbin Reservoir with up to fifty birds sighted in winter months and more than six breeding pairs currently established.

Great blue herons suffered along with many other showy waterfowl because of the collecting of feathers and the deterioration of wetlands and water quality. Now afforded protection and with improved water quality, heron populations have rebounded. Furthermore, the recent increase of beaver has exerted a profoundly positive effect on great blue heron, which utilizes the resulting dead trees and habitat in flooded beaver ponds.

Openland Species Increasing with Forest Clearance and Agriculture

Forest clearance and the creation of openland habitat favored many native species that were uncommon in the forested landscape. This land-cover transformation may also have enabled grassland and shrubland species from regions including the Midwest to immigrate to New England. Species including reptiles, amphibians, diverse birds, and mammals such as the red fox, striped skunk, New England cottontail, and woodchuck peaked in abundance with maximum agriculture or during the early period of farm abandonment and forest recovery. Although exhibiting diverse population trajectories according to their habitat preferences for, for instance, grass height and density or abundance of woody vegetation, most of these species are continuing to decline as forests mature and remaining open and successional habitats become woody or are developed for human uses. As a consequence, this group includes some of the most vulnerable populations in the Northeast.

In many ways the most dramatic and interesting examples of favorable responses to historical land-use practices are witnessed in grassland bird species (Figures 7.5 and 7.6). Indeed, species such as upland sandpiper, vesper sparrow, grasshopper sparrow, meadowlark, bobolink, and savannah sparrow are a major focus of environmental concern that present a substantial management challenge and interesting ethical issues for conservationists.

The early history of these birds is uncertain. Like most passerines and nongame species, they were not recorded from Massachusetts until the publication of Peabody's *A Report on the Ornithology of Massachusetts* in 1839, which was the first attempt at a comprehensive bird list for the state. Consequently, their native status is uncertain. There is no doubt, however, that these birds proliferated in the agrarian landscape. Their response and timing of peak abundance undoubtedly varied because of subtle differences in nesting and foraging habitat. Through the height of agriculture (1830–70), the upland sandpiper, which uses large grassy areas with low vegetation, was recorded by Thomas Nutall and others as "common in Worcester County in the summer" and "abundant across the state." This is the only game species of the six and is thought to have expanded eastward from natural prairies and peaked in the mid-1800s, when it was hunted in large numbers. Vesper sparrows were so plentiful in open fields and upland pastures from Cape Cod to the Berkshires that E. H. Forbush in 1907 considered them to be the "most abundant ground sparrow in Massachusetts" after the song sparrow. The grasshopper sparrow apparently peaked slightly later in the late nineteenth century and, though never common, could be found in "spectac-

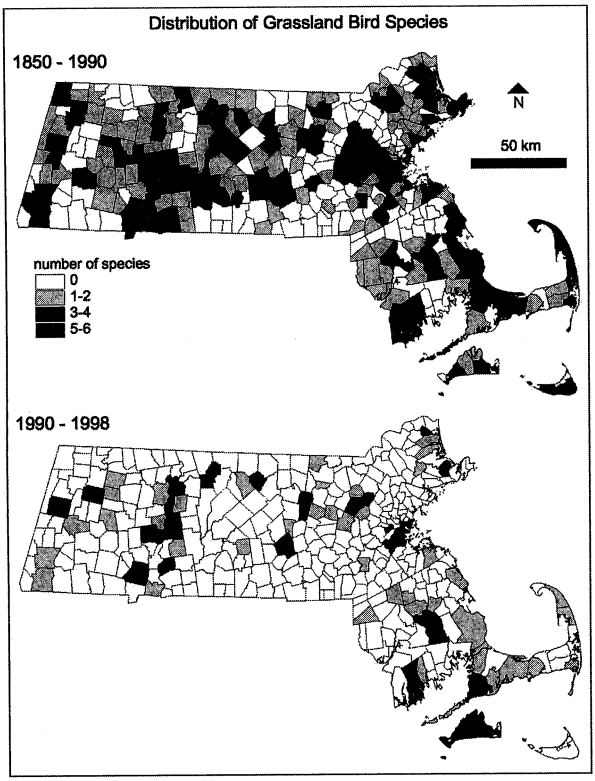


Figure 7.5. Historical and modern distributions of important grassland bird species in Massachusetts. The six species include bobolink, eastern meadowlark, savannah sparrow, vesper sparrow, grasshopper sparrow, and upland sandpiper. A broadscale reduction in distribution and abundance of all species occurred with reforestation and the loss of open and successional habitats, making these species high priorities for conservation. The status of these grassland species in Massachusetts at the time of European settlement is unknown, but most were probably quite uncommon. Reprinted from Foster, Motzkin et al. 2002.

ular abundance" on Cape Cod, Nantucket, and Martha's Vineyard and in lower numbers across the state. This remarkable upswing in now uncommon species was paralleled by some of the more familiar birds of New England's agricultural past—such as the bobolink, meadowlark, northern bobwhite, red-winged blackbird, and bluebird.

These species thrived with traditional, low-intensity agricultural practices, including extensive grazing and mowing, and they declined as open fields and pastures reverted to forest. Considered a delicacy and avidly hunted in the late nineteenth century, the upland sandpiper declined first, but by the mid-twentieth century the number of breeding sites for all grassland species was declining statewide. In the 1950s, up-

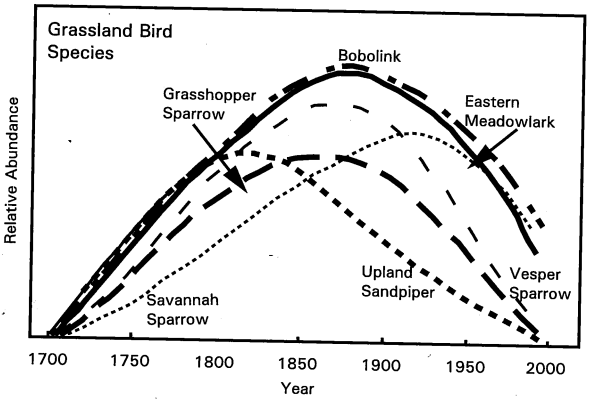


Figure 7.6. Inferred changes in the population size of important grassland bird species in Massachusetts through time. The native status of some species is uncertain. Reprinted from Foster, Motzkin et al. 2002.

land sandpipers were located in only a few localities, and by the 1970s and 1980s the three species were depending largely on artificial, highly humanized landscapes, primarily military bases, airports, and landfills. Currently the upland sandpiper is listed by the Commonwealth of Massachusetts as "endangered," whereas vesper and grasshopper sparrows are "threatened."

Ironically, ten of the eleven most important refuges for these species are industrial or military sites, where the species are being maintained only through the coordinated efforts of managers and conservation agencies to regulate mowing and burning regimes and to control disruptive human impacts. Although these species are essentially unknown by the general population, their remarkable historical dynamics, their imperiled statewide status, and their reliance on artificial habitats make them important examples of the fascinating interface between policy discussion and historical-ecological research.

Extirpated/Extinct Species

The loss of wildlife species receives considerable attention from ecologists and conservationists who seek to understand their former roles in the landscape and the effect that their disappearance exerts on current ecosystem processes. In particular, historical perspectives may provide insights into the importance of individual species for the coherence of species assemblages as well as the concept of keystone species. Remarkably, despite the massive impacts of land use, land-cover change, and human exploitation on the northeastern United States, relatively few species of plants or animals were driven to extinction. Arguably the

two most important examples of colonial extinctions from the temperate forests of New England are the passenger pigeon, which was remarkably widespread and abundant, and the heath hen, which was of much lower and more localized distribution.

In contrast, a relatively large group of species remains regionally extirpated but represents potential candidates for reintroduction. Although some of these species, such as wolverine and lynx, were uncommon, were near the edge of their ranges, or were eliminated early in colonial history, a few larger predators, notably wolf and cougar, were well established and persisted into the nineteenth century. Large carnivores are underrepresented in the modern landscape but might play a key role in controlling the populations of other species and thereby influencing forest conditions. Consequently, ecological, management, and cultural ramifications of their reintroduction are increasingly discussed.

Wolves have large ranges but are habitat generalists that prefer areas with low human densities. Although their diet primarily consists of large prey such as deer, moose, and beaver they are opportunists that will feed on rabbits, other rodents, a range of small mammals, and carrion. At the time of European settlement, the gray wolf was widespread and relatively abundant across New England (Figure 7.7). However, a concerted effort to eliminate the species began almost immediately after settlement; this, combined with land-cover changes and a decline in prey species, eliminated wolves on a broad scale. The first wolf bounty was established by the Massachusetts colony in 1630, and subsequent local bounties increased this incentive and fueled active extirpation. Between 1650 and 1655, bounties were paid on 147 wolves. This number increased thereafter to a peak in the 1650s when more than 1,000 wolves were killed in four years. Although 3,043 bounties were paid between 1700 and 1737, declining populations were reported across the state, and some local bounty statutes were repealed. Intact wolf populations were apparently restricted to the Berkshires and Cape Cod at this time, prompting retention or increases in bounties in those areas. By the early nineteenth century, wolf killings became uncommon and notable in local lore. During this period, many towns noted their last sightings. A wolf that reputedly killed 3,000 sheep in the area near the base of Cape Cod over a four-year period was killed by a Sandwich man in the 1830s. This may have been the last of the species in Massachusetts.

Natural Range Extension

Throughout the historical period, but increasingly in the twentieth century, several wildlife species have naturally expanded their ranges into Massachusetts, including at least two mammals (the eastern coyote and Virginia opossum) and numerous birds that have become abundant (for example, turkey vulture, northern mockingbird, tufted tit-

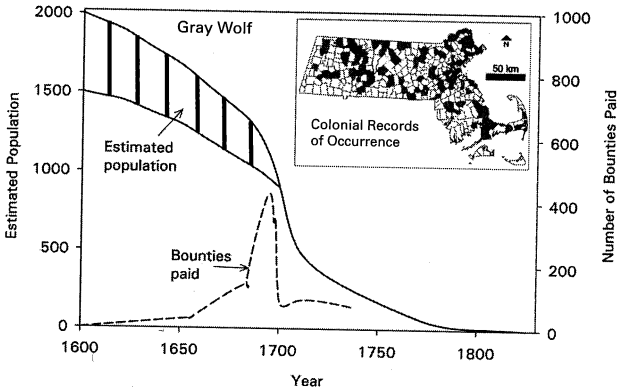
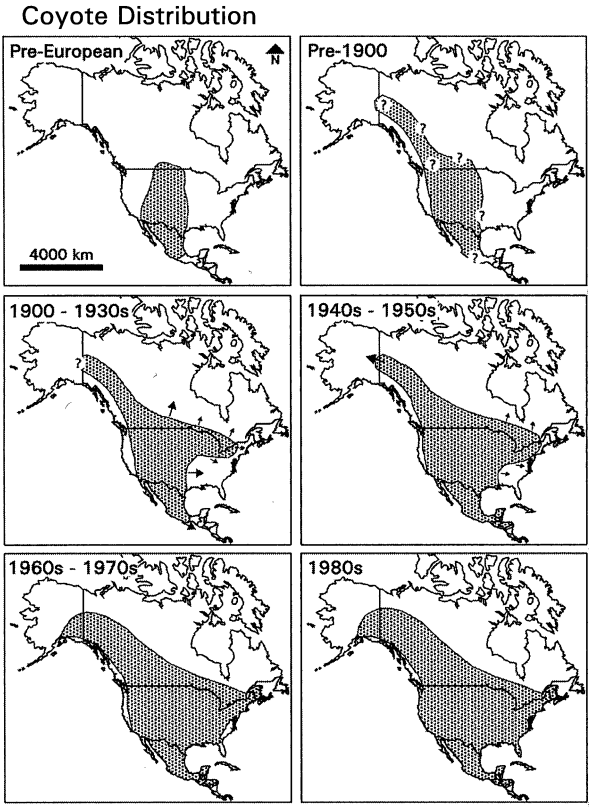


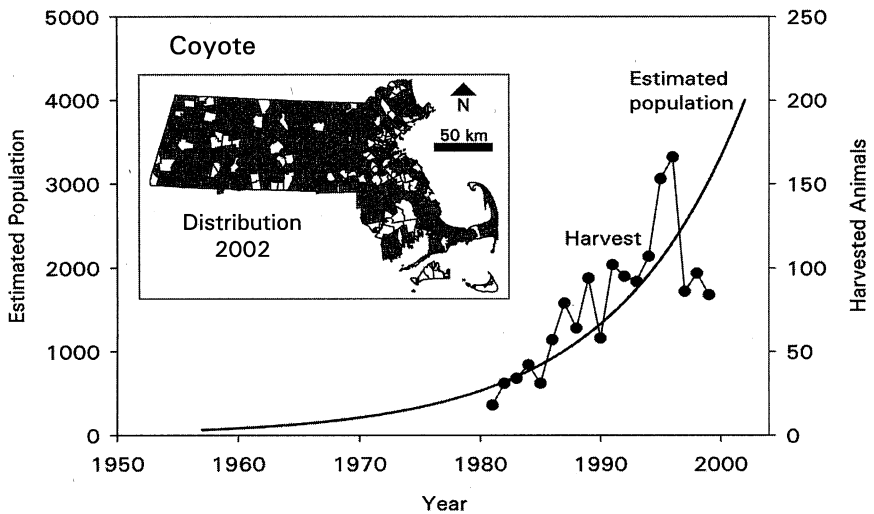
Figure 7.7. Historical distribution and decline of the gray wolf in Massachusetts. The species occurred statewide, with the exception of the coastal islands, before its eventual extirpation. Reprinted from Foster, Motzkin et al. 2002.

mouse, and cardinal). Factors underlying these expansions vary as they occur from all directions and include species with diverse habitat preferences and life histories. However, causes likely include changes in climate, the availability of new food resources (for instance, winter birdseed and roadkill), changes in competition and predation, and changes in habitat and land cover. Among these species, however, the coyote has had the most remarkable, continental-scale expansion and probably exerts the greatest influence on forest ecosystems (Figure 7.8).

Before European settlement, coyotes ranged the western prairies from central Mexico to southern Canada. With changes in land use and other wildlife, especially dramatic declines in wolves, which are predators and competitors of coyotes, coyotes began expanding significantly in the nineteenth century and moved slowly eastward. Coyotes reached Massachusetts by the late 1950s, when the first animals were shot in the western part of the state. The new population rapidly expanded in size and geographical area, reaching 500 by 1979 and an estimated 3,000 to 4,000 in 1996. Although a coyote hunting and trapping season was initiated in 1981, the number of animals killed each year is relatively low, and the species now occupies the entire state except for a few of the coastal islands. Currently, the population is continuing to increase.

Although the coyote represents the first large canine predator to roam the Massachusetts landscape widely in nearly three centuries, it does not replace the wolf ecologically. Eastern coyotes are larger and do have a greater tendency toward packlike behavior than their western counterpart. Nonetheless, they are smaller than wolves; are more adaptable to a range of habitats, including human environments; and typi-


Coyote Distribution
Pre-European
N
4000 km
Pre-1900
1900 - 1930s
1940s - 1950s
1960s - 1970s
1980s


Coyote
N
50 km
Distribution
2002
Estimated
population
Harvest
Estimated Population
Harvested Animals
Year
5000
4000
3000
2000
1000
0
250
200
150
100
50
0
1950
1960
1970
1980
1990
2000

cally forage on smaller prey, such as rodents, birds, amphibians, and small mammals. Eastern coyotes do take deer, though the magnitude of this activity is uncertain; despite this, coyotes appear to lack the capability of controlling the population growth of large animals such as beaver, deer, and moose that were historically preyed on by wolves, cougar, and Native Americans.

Introduced Species

As a consequence of intentional or accidental introductions, a wide range of organisms, from microbes to mammals, have been added to the state's biota. Although most introductions fail or have only local effects, a number have led to widespread populations that have exerted major impacts on natural ecosystems. The earliest introductions were accidental, including the house mouse and black rat, two species that have become common. A second group was game animals, primarily fish and a few birds, introduced to replace disappearing native species in intriguing attempts to fill what were perceived as vacant niches, or in an effort to provide new hunting and fishing opportunities. Rainbow trout, European brown trout, and carp are examples of nonnative species that were stocked from hatcheries and have established naturalized, reproducing populations. Similarly, pheasant, eastern cottontail, black-tailed jackrabbit, and European rabbit have maintained low to widespread populations as a consequence of intentional, and in some cases (for example, pheasant) persistent, human efforts. Ironically, the same public agencies that today try to restrict the introduction of exotic plant and animal pests were responsible for the active introduction and maintenance of nonnative game species. The ecological consequences of these introductions are poorly understood as research effort has been focused on successful establishment rather than attendant consequences to habitat quality or native species.

Finally, driven by a range of motivations, numerous nongame bird species have been introduced and naturalized. One notable example is the European starling, which was released into New York's Central Park in 1890–91 as part of an attempt "to introduce all of the birds mentioned in Shakespeare's plays." Reaching Massachusetts in the early 1900s, the population peaked at more than 500,000 by the 1930s but has subsequently declined somewhat, apparently due to winter mortality. Another common species, the house sparrow, was released in 1858 and

Figure 7.8. Range extension of the coyote and its local increase in population in Massachusetts. The coyote is expanding and is currently the largest top predator in the region. Reprinted from Foster, Motzkin et al. 2002; North American maps modified from Moore and Parker 1992, with permission from G. Moore.

then introduced in 1868–69 in an attempt to reduce gypsy moths and other insect pests. Although the species peaked between 1890 and 1915, it is still common and widespread and is considered disruptive to native species, including the eastern bluebird.

Persistent Species

In contrast to the long-term directional dynamics discussed above, numerous species have remained relatively common over the past 300 years despite periodic fluctuations. For example, raccoons have fluctuated with trapping, severe weather, and disease, such as the rabies epizootic in the early 1990s; porcupines presumably varied with changes in forest cover and predators, including the fisher; and bobcat populations have changed with prey availability, including rabbits. Similarly, crows and gray squirrels have been reported as common from the days of Thomas Morton and William Wood to the present, despite bounties from the mid-1600s to the 1800s. Interestingly, the gray squirrel population dropped sharply between 1910 and 1920, evidently in response to the widespread mortality of chestnut trees, which succumbed to the blight that was spreading across the land. Squirrels disappeared completely in some localities, for example becoming rare in Petersham for more than two decades. However, they recovered strongly in the 1930s, and the species is apparently as abundant and widespread today as before the blight. Overall, these and many other species exhibit no major long-term trends.

Ecological Implications and Social Consequences of Wildlife Dynamics

It is apparent that wildlife populations have been highly dynamic in response to historical changes in landscape conditions and habitat availability, active human persecution, and a range of indirect activities of people. An understanding of these dynamics provides a useful background for policy decisions and affords interesting insights into the functioning of the forest landscape of New England.

A basic question emerging at the community level for both plants and animals concerns the coherence of species assemblages through time. At the most fundamental level, ecologists are interested in whether assemblages of plant and animal species exhibit continuity through time or whether species operate fairly independently of one another. Although natural history texts are replete with examples of tight relationships among specific sets of species (for example, specialized plants and their animal pollinators; predator-prey cycles), the question remains whether such examples are representative of broad interrelationships or whether the majority of species actually form loose and highly mal-

leable associations. Paleoecological and archaeological studies of plants and animals indicate that through the postglacial period, individual plant and animal taxa responded quite independently to the many different climatic and environmental changes and settings that arose. Necessarily, such individualistic behavior resulted in a sequence of quite different assemblages of organisms through time. Thus, the very long-term, though incomplete, postglacial record indicates that the suites of species that we see in the landscape today are novel and have no great historical continuity.

The historical data on changes in wildlife distribution and abundance certainly confirm this pattern. Clearly there are strong interactions among many species, and historical studies yield examples of patterns of change over time that may be generalized for groups of species. However, it is also clear that each species is unique in its dynamics, that animal distributions and assemblages have changed continuously through time, and that modern conditions and modern assemblages of organisms are distinct. Few species exhibit closely linked dynamics, as each responded independently to the unusual combinations of habitat and human activity that the landscape experienced in the past 200 years. Although this individualistic behavior may be accentuated by the selective focus of humans on specific animals—either promoting or persecuting them—it is apparent that the linkages among the organisms that we have examined are relatively loose.

Drawing this observation and the individualistic notion together, we can conclude that the very natural appearance of the modern forest landscape, including its populations of coyotes, fishers, bears, moose, deer, and turkeys, is culturally conditioned and is not analogous to presettlement conditions. Thus, the process of forest growth and the return of many forest animal species is very different from a simple restoration of past conditions. Though perhaps obvious on serious reflection, recognition of the strong element of direct and indirect cultural control over our modern landscape is critical for successful conservation and ecological understanding. Conveying the scale of recent dynamics and their linkage to human and landscape history is also a critical element in public education and ongoing policy development.

The changes that have occurred recently in wildlife populations, including the reappearance of moose, fisher, and bear in much of New England, remind us of the sizable and important lags that are inherent in ecological response; they also alert us to anticipate future changes, even if additional human activity were to cease (Figure 7.9). Forests, once established, take decades or centuries to mature; similarly, animals, even when highly mobile, require time to migrate and expand their populations when the landscape, environment, or cultural setting changes. Examples like turkey, beaver, coyote, and white-tailed deer illustrate this process and underscore the potential changes that await the moose, os-

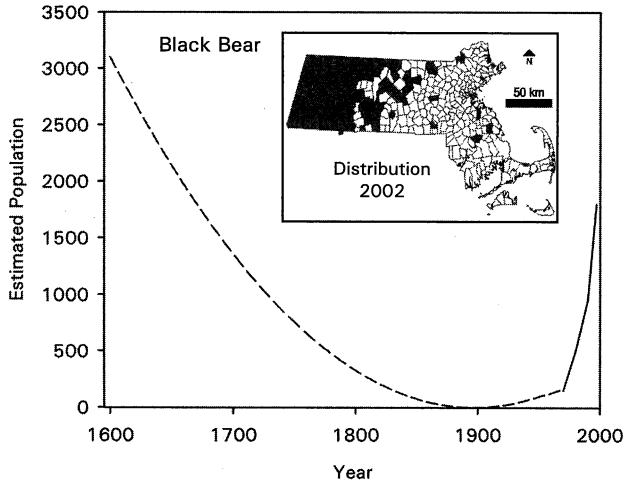


Figure 7.9. Historical dynamics and major recent increases in bear populations in Massachusetts. The species continues to expand its range eastward from local populations that persisted in the nineteenth century in the western part of the state and is increasing at approximately 8 to 10 percent annually. Reprinted from Foster, Motzkin et al. 2002.

prey, bear, eagle, and great blue heron populations. However, population growth is also strongly affected by mortality. Hunting is especially effective at controlling population growth where population levels are low, as was true for white-tailed deer through much of the twentieth century.

The New England landscape, which has already changed quite dramatically in the past century, is undergoing additional alterations as the plants, animals, and ecosystem processes respond slowly to changes in historical disturbance and habitats. Indeed, the historical perspective underscores the fact that wildlife assemblages at any given time are composed of species undergoing strikingly different trajectories. Many animals that can thrive in our newly reforested and maturing landscape are well-established; some are just arriving and becoming established and are poised to flourish; others are yet to arrive but may eventually get here naturally or through human intervention and may yield unforeseen impacts. In contrast, species that were common in our agricultural past are in the process of a long decline that may be inevitable as a consequence of ongoing changes in the condition of the landscape. Therefore, at any given time the assemblage of animals on the landscape includes many species, each of which is on a different ecological trajectory in response to past and ongoing changes: some are increasing, some declining, others perhaps are exhibiting few changes. In order for ecologists to evaluate species' roles or for conservationists to develop effective man-

agement strategies, it is critical to be able to identify the specific trajectory associated with each species.

Ecologically, many questions and challenges still remain in our understanding of the consequences of the wildlife dynamics that we have highlighted. Currently, at least twenty large or important forest species that were present at the time of European settlement are absent from New England. It is challenging enough to determine the role and influence of new species that have arrived such as coyote, but how do we evaluate the consequences of the absence of historically important species on the functioning of modern ecosystems? What role did passenger pigeons play in the dispersal of trees and the dynamics of New England forests, and how would our landscape differ in the presence of million-bird flocks and their dense and extensive roosts? What impact would the reintroduction of wolves or cougar have on other animal populations, and, in turn, how would these effects ripple out into the structure, composition, and function of the forests? What effect will an expanding moose population have on forest regeneration, understory composition, and nutrient cycles? As we draw on paleoecological and historical data for our understanding of long-term forest dynamics, how do we incorporate our emerging knowledge of the faunal changes that have occurred? The loss and the addition of new species provide an unusual opportunity, and an important research mandate, to investigate the role that individual species play in the structuring and functioning of ecosystems.

On the cultural and policy side, awareness of the magnitude and rate of wildlife changes over time provides a useful perspective for conservation and management. On the basis of past changes and trajectories, we can anticipate future declines in some species, major increases in others, and some of the consequences of newly arriving species. Clearly, at least two major and interrelated issues face wildlife managers. Foremost is the observation that the trend toward a more forested and wild landscape with large forest animals along with an expanding suburban human population will lead to increasing conflicts between human safety and appreciation for wild nature. At the very least, this means we need to educate people about wildlife, nature, and its history and modify some of our behaviors, such as removing bird feeders in the early spring when the bear population emerges from winter dens. In the case of many of the larger mammals (for example, bear, moose, beaver, and coyote) the social carrying capacity of the landscape (that is, the density and distribution of a species that humans can tolerate or accommodate) is ironically declining as the natural carrying capacity of the land is increasing. Modification of human behavior would enable greater populations to be tolerated more safely. Second, because the modern fauna is dominated by relatively few, large species and lacks major predators, we need to provide more ability to control wildlife populations, either

through direct management or through well-conceived introductions of additional species. This is a formidable task for a human population that is generally poorly informed about nature and wildlife dynamics and is largely opposed to the most ready means of wildlife regulation: hunting and trapping.

Wildlife brings immeasurable ecological and social benefits but may also disrupt and damage human property and occasionally even pose direct or indirect threats to the health of humans, as well as domestic animals. Beavers cut trees and flood cellars, roads, and sewer systems; deer and moose can alter forest composition, damage human property, and present a major hazard on highways; coyotes and bears may become too accustomed to people for the welfare of either species; and a range of diseases from giardiasis and Lyme disease to rabies and West Nile virus can be transmitted or promoted by animal vectors. Current U.S. expenditures to deal with Lyme disease alone are estimated to exceed $500 million per year, and southern New England states such as Connecticut experience as many as 75,000 cases of the disease annually.

Evaluating the benefits and costs of wildlife and developing socially acceptable measures of control will be a major challenge for New England's future. The evaluation of historical trends, although it may supply few direct solutions, can assist in defining the issues, anticipating conflicts, and developing strategies for long-term changes. A historic perspective can also provide intriguing insights that aid in informing managers, the public, and scientists of some of the major changes that are occurring around us.