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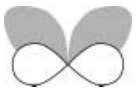

Wildlife dynamics in the changing New England landscape

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Abstract

Aim Over the past four centuries the eastern US has undergone remarkable landscape and land-use transformations involving deforestation, intensive agriculture, farm abandonment, reforestation and human population increase that have induced sweeping changes in wildlife assemblages, abundances, and distributions. This study compiles data on major wildlife species and seeks to identify broad population trends and to address both fundamental and applied questions regarding these long-term patterns.

Location The study encompasses the state of Massachusetts, which is broadly representative of the habitat conditions and landscape and cultural history of other New England states.

Methods A wide range of historical sources of data were used including town histories, newspaper and other popular accounts, scientific studies, museum collections, compiled trapping, bounty and harvest records, explorer accounts, and agency records. Statewide distribution maps and generalized population trends were assembled for individual species where practical, and major trends in species trajectories were identified. Emphasis was placed on mammals and birds for which data are readily available.

Results Although species exhibited highly individualistic long-term dynamics in response to habitat change and human pressure, six major trajectories of species changes are identified: (1) large mammals and birds that declined historically and increased recently, (2) open-land species that went from low to high abundance with the creation of open habitat but are in rapid decline today in the heavily wooded landscape, (3) species regionally extirpated or globally extinct, (4) species expanding their range from the west, north and south, (5) non-native, introduced species, and (6) persistent species not exhibiting major long-term trends. Currently, wildlife populations are changing at a remarkable rate leading to significant ecological impacts on the landscape and many other species, creating major conservation and management challenges, and generating novel and oftentimes significant conflicts with human values.

Conclusions The rate of historical and current changes in wildlife assemblages pose many scientific and conservation challenges, especially in this heavily forested but highly populated landscape. Historical data are fragmentary and oftentimes uncertain, modern information on wildlife populations is similarly incomplete, and small populations of species that are immigrating, expanding or declining from previously high levels pose major sampling problems; development of conservation and management plans for rapidly expanding populations of large woodland mammals (e.g. moose, coyote, deer, bears, beaver) and for declining populations of cherished species that are dependent on

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cultural landscapes generates conflicting directives; and educating, and modifying the behaviour of a human population that is living in but separated from nature is a difficult enterprise. The future is guaranteed to bring major dynamics in these historically novel species assemblages.

Keywords
Wildlife, animal populations, land use, habitat change, Massachusetts, New England.

INTRODUCTION

'Research programs pay too little attention to the history of wildlife… We do not yet appreciate how much historical evidence can be dug up, or how important it can be in the appraisal of contemporary ecology.' Aldo Leopold (1933).

'The abundance of wildlife does not result from jurisdiction, sportsman's meetings or bureaucratic dictates; it results from what we do with the land.' E. H. Graham (1947).

Although reforestation and associated land-cover changes in New England since the height of agriculture in the nineteenth century were dynamic, they occurred gradually within the human or research time-frame and therefore were easily overlooked by most casual or even trained observers (Fig. 1; Hall *et al.*, 2002). The same cannot be said of the recent transformation that has taken place in the wildlife of New England and much of the eastern US (Foster, 1999). In past decades, nearly daily newspaper and magazine articles have highlighted remarkable changes in animal populations as well as numerous conservation and social issues that have accompanied these (DeGraaf & Miller, 1996; Sterba, 2002).

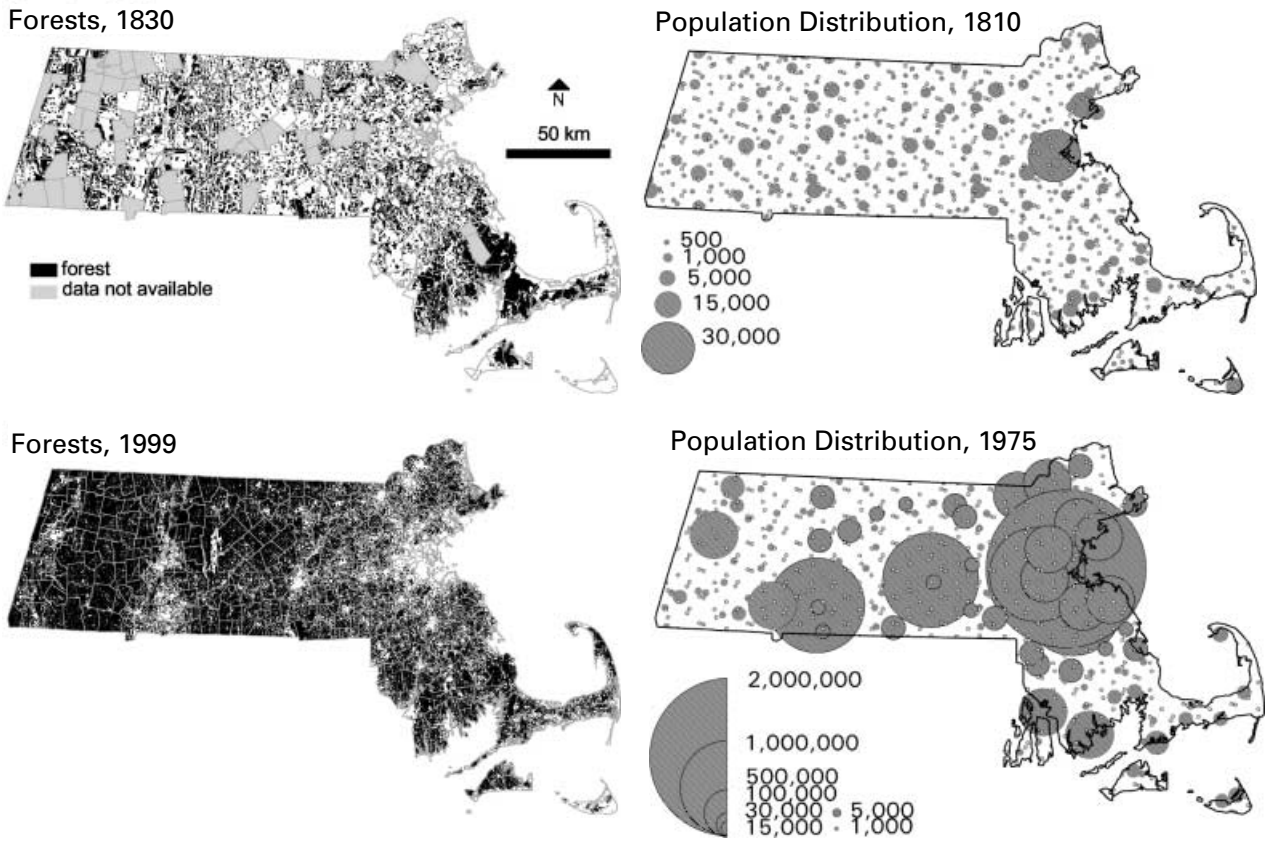

Figure 1 Maps of forest cover and human population distribution in the state of Massachusetts in the nineteenth century (near the height of agricultural activity and forest clearance) and the modern landscape. Data from Hall *et al.* (2002), MassGIS (unpubl.) and the US Census.

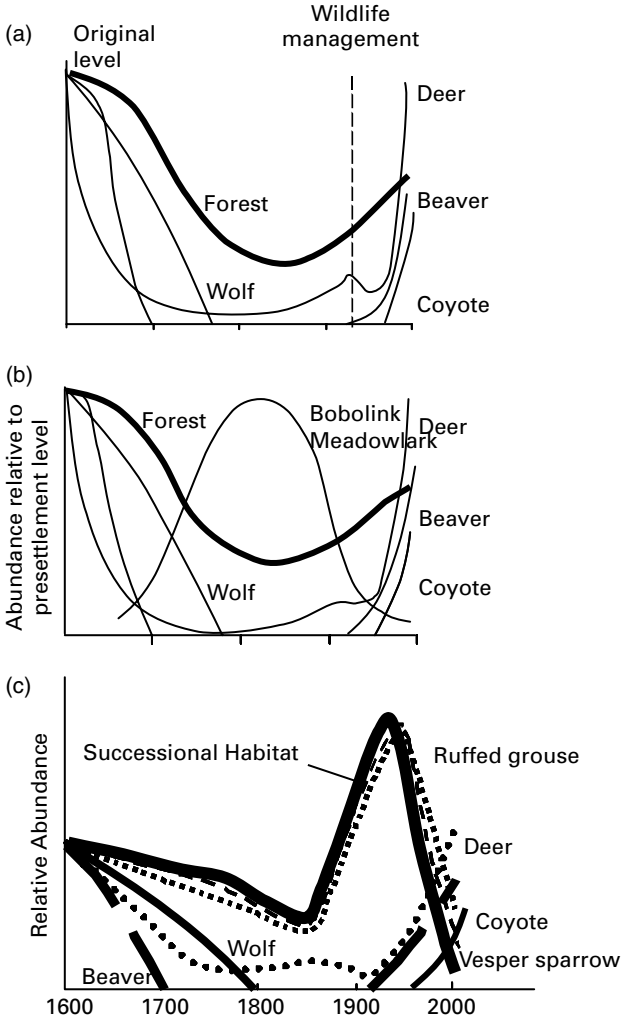

Figure 2 Three related but contrasting depictions of land cover and wildlife dynamics in New England that highlight the important role that historical research plays in the interpretation of modern conditions and the development of management approaches. The bottom figures (b, c) are 'modified' from the top figure (a). Bickford & Dymon (1990; a) and Foster (1995; b) emphasize the forested nature of New England at the time of European settlement and trajectories of forest dwelling species in response to deforestation and depredation. Bickford, commissioner of Massachusetts Fisheries and Wildlife, also highlights wildlife management in the recovery of some species. Foster adds openland species, typified by bobolink and meadowlark, and interprets them as increasing historically from low densities in response to deforestation and agriculture (cf. Motzkin & Foster 2002). In contrast, DeGraaf & Yamasaki (2001; c) interpret the pre-European landscape as 50% successional and open habitat and consequently de-emphasize the abundance of forest dwelling species. In this view successional species such as ruffed grouse and vesper sparrow are interpreted as declining with European settlement but then reaching a historical peak coincident with early twentieth century reforestation and succession. Whereas Foster (1995) interprets the declining abundance of openland and early successional species in the modern landscape as reversing the early historical trend, DeGraaf & Yamasaki (2001) depict these species as recently reaching their lowest abundance in the last 400 years. Consequently, the former argues that openland species require management simulating historical agricultural practices, whereas the latter suggest that management should simulate natural disturbance and Native American practice.

Many large mammals and birds that have been uncommon for decades or even centuries such as bear, beaver, fisher, turkey, moose, eagles, herons and vultures are increasing and are regularly encountered in backyards, along roadsides, or on wooded paths (Foss, 1992). In contrast, familiar and cherished bird species of New England's past, including bobolinks, meadowlarks, woodcock, and whippoorwills are declining or have disappeared over broad areas and are the focus of major restoration activities (Fig. 2b; Droge, 1998). 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, conservationists, wildlife managers, and citizens are confronted with major scientific questions, policy issues and ethical dilemmas. What kinds of changes are actually occurring and how long have they proceeded? Are there generalizable patterns in species trajectories and

causal factors associated with them? Do long-term data on these dynamics improve our understanding of the broad-scale organization of wildlife assemblages? How can these ecological insights inform policy as we decide which species to manage for, as we seek effective approaches to achieve these objectives, and as we anticipate further changes?

A historical perspective may assist in educating and even modifying the behaviour of the human population that interacts with this dynamic wildlife (cf. Berlik *et al.*, 2002; Motzkin & Foster, 2002; Foster & Motzkin, 1998). In a region with immense tracts of maturing forest, but a largely suburban population that is disconnected from the natural landscape, the range of issues involving wildlife extends from the desire on the part of many conservationists to restore large mammals such as fisher, wolves, moose and even wolves, to a new appreciation for nature by the general population, to concerns for human safety and personal property as a result of the activity of a handful of species (Leahy *et al.*, 1996).

In order to address these issues, there is a critical need for long-term data interpreted within a broad perspective on New England landscape change (Fisher, 1933; Leopold, 1933; Foster, 2002). Such an approach to conservation issues also offers an opportunity to answer basic ecological questions about the factors controlling wildlife assemblages, the nature of major feedbacks between animal species and their habitats, and the contrasts between the organization and dynamics of wildlife and plant assemblages.

In pursuit of a long-term perspective on wildlife dynamics we collected historical data on animal populations for the state of Massachusetts in southern New England and analysed these in order to: (1) document the major trends in wildlife populations since European settlement, (2) identify the losses or arrivals of species and related shifts 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 landscape processes through time, and (5) provide a context for interpreting current changes and for guiding conservation policy.

APPROACHES AND METHODS

The geographical area, timeframe, and species investigated in this study were selected with regard to ecological and pragmatic considerations. The compilation of hundreds of years of historical records from diverse sources requires the identification of a common geographical reference area (cf. Cogbill *et al.*, 2002; Hall *et al.*, 2002). Most historical wildlife records pertain to specific political units: e.g. state agencies provide the most comprehensive recent data whereas town records and histories, which may be aggregated to a state level, provide critical information for the early colonial period. In consideration of the spatial coverage of essential historical records a statewide analysis was selected. As much of the legislation and management concerning wildlife originates at a state level, the resulting data and analyses may also be relevant to major policy needs. However, as data sources and temporal coverage vary considerably among adjacent states and are oftentimes difficult to aggregate we limited our analysis to a single state: Massachusetts. This land area incorporates fairly large environmental, vegetation and cultural variation that is broadly representative of New England and much of the northeastern US (cf. Cogbill *et al.*, 2002; Hall *et al.*, 2002).

Data sources

Data from numerous sources were incorporated into a statewide GIS and data base that also includes extensive modern and historical information on land use and land cover (Hall *et al.*, 2002). Unfortunately, archaeological data for the state are inadequate for an analysis of pre-European faunal use and distribution comparable with that possible at a continental scale (cf. Graham, 1992; Faunmap, 1996). Consequently, early species lists and distributional information come from explorers' accounts, town and state legislation, bounty and harvest records, natural histories, scientific studies, museum collections, newspaper and other popular accounts, and town and county histories. Although varying in taxonomic detail, data density, and accuracy, these sources provide a strong qualitative to semiquantitative picture of the changing abundance and extent of wildlife populations over the first few centuries following European settlement. In particular, published histories of the more than 300 towns in the state, mostly written between the mid-1800s and mid-1900s provide information including species lists, bounty records, anecdotal descriptions of wildlife populations, and dates of first and last observations. The large number of towns and observations help to compensate for the spatial and temporal gaps in individual records and enable fairly robust interpretations of major changes through time. In addition, species-specific studies and historical reviews in student theses and agency research and management documents often include extensive background on historical trends, ecology, behaviour, and status of individual animal species. For the past century data including population estimates, harvests, accidental deaths (e.g. road kills), sightings, introductions and related management activities have been 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 melding ecological and conservation interests with pragmatic constraints, this study focused on species that are ecologically important, of social and conservation concern, and well represented in historical records (Appendix 1). Consequently, treatment is biased towards mammals, game species, large birds, persecuted 'vermin' species, and selected notable taxa of specific conservation focus. Songbirds, amphibians, reptiles, fish, small mammals and invertebrates are largely excluded because of their incomplete representation in historical data.

CULTURAL AND ENVIRONMENTAL SETTING FOR HISTORICAL WILDLIFE DYNAMICS

Little information exists on wildlife in New England during the Late Woodland Indian period (*c.* 1000–1500 AD, Chilton, 1999, 2000, 2001, and pers. comm.). Nonetheless, the landscape was changing continually as a consequence of climate change and natural disturbance (Foster *et al.*, 2002a; Parshall & Foster, 2002, Parshall *et al.,* 2003) and human activity certainly influenced animal populations well before European settlement in 1620. Indian populations were concentrated in coastal and riverine areas, but hunted regionally for terrestrial, freshwater, and marine wildlife (Bragdon, 1996; Hodgkins, 2000). Wildlife abundance was locally altered through habitat modification by fire and clearing for encampments (Cronon, 1983; Motzkin & Foster, 2002). Indeed, in an extreme view Native Americans have been a major factor modifying the composition and abundance of many animal species since deglaciation (Martin & Klein, 1986; Kay, 1994; Krech, 2000).

The earliest Europeans–explorers, trappers, settlers and traders–exerted such an immediate and profound impact on the land, Indian populations, and wildlife that even the oldest historical descriptions depict New England's animal populations and landscape in major transition (Brokaw, 1978; Bragdon, 1996; Chilton, 2000; Motzkin & Foster, 2002). Diseases that decimated and altered the social structure of Indian populations undoubtedly exerted an indirect effect on wildlife through decreased hunting pressure and alteration of wildlife habitat around encampments (cf. DeGraaf & Yamasaki, 2001). Trapping had a more substantial although selective impact, as it generated a widespread decline in valuable fur-bearers across and beyond Massachusetts and New England (Thompson, 1853; Russell, 1980; Allen, 1992; Terrie, 1993). Consequently, the early colonial landscape that is routinely used as a baseline for historical studies was actually remarkably dynamic (Ceci, 1975; Bragdon, 1996). Habitat conditions and the status of individual species could change rapidly between descriptions and might easily differ between the archaeological and ethno-historic records (cf. Motzkin & Foster, 2002).

Historical land-use varied with physiography and distance from the coast, urban centres and agricultural regions like the Connecticut Valley (cf. Russell, 1982; Foster & O'Keefe, 2000; Hall *et al.*, 2002). The clearing of forest proceeded most rapidly and extensively in the Eastern Lowland and Connecticut Valley. The rough and distant Berkshire Plateau in the western part of the state was settled last and supported large forest tracts in the nineteenth century. However, the greatest density of forest persisted less than 50 km south of Boston at the base of Cape Cod where agriculture was limited because of dry, sandy conditions (Hall *et al.*, 2002). Utilitarian attitudes prevalent through the early centuries after settlement led to heavy harvesting of many taxa, sustained efforts to eradicate 'vermin' species, and widespread environmental degradation (Thompson, 1853; Matthiessen, 1959; Whitney, 1994). Accompanying the shift from an agrarian to industrial economy in the nineteenth century, there was an increase in market hunting, trade in feather for millinery uses, and collection of natural history specimens.

With agricultural decline, forests expanded although unevenly across the state (Hall *et al.*, 2002). Farms persisted in the broad lowlands, whereas forest area increased most rapidly and completely on the uplands and in the western part of the state. The late nineteenth century brought new appreciation for wildlife, including conservation, and a sport hunting ethic. Professional wildlife management focused on game species and led to the creation of the Commission on Inland Fisheries in 1866, which was granted broader authority in 1886 to become the Massachusetts Commission on Fish and Game. This statewide agency initiated licensing, hunting and fishing regulations, and a range of species introductions.

Through the twentieth century as Massachusetts has become increasingly populated, human distribution, land cover, and wildlife habitats have become more heterogeneous (Fig. 1). The Berkshire Plateau and northern Worcester County remain relatively undeveloped and forested; eastern and south-eastern Massachusetts are intensely fragmented by roads and development; Cape Cod and the coastal islands are undergoing rapid population growth and the Connecticut Valley juxtaposes farm fields, housing, and industry with wooded swamps and isolated, forested mountains (cf. Hall *et al.*, 2002). Statewide, forest area peaked in the 1980s, but forests continue to mature and harvesting remains haphazard and moderate in intensity (Berlik *et al.*, 2002). Development, suburban fragmentation, and 'parcelization' (progressive reduction of forest lot sizes) continue, particularly in eastern Massachusetts (Steel, 1999). Meanwhile social attitudes towards wildlife are shifting from conservation to preservation particularly through open-space acquisition and protection (Dizard, 1999). The major agency overseeing fish and wildlife activities (Division of Fisheries and Wildlife) now includes an active programme focused on the conservation of non-game species (Natural Heritage and Endangered Species Programme). Other state and federal agencies, and private environmental organizations are also focused on monitoring, management, and educational programmes addressing broad wildlife issues.

RESULTS

General trends in wildlife dynamics

Historical data for nearly one hundred 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 (Fig. 2 and Appendix 1).

(1) A large group of species, including many large mammals and birds that were extensively hunted or require broad

areas of mature forest habitat, exhibit a long-term historical pattern of decline and recovery. These species were widespread at European settlement, decreased in the seventeenth to eighteenth century and were locally to regionally extirpated by the mid-nineteenth century. Over the past century and in distinctively individualistic patterns, they have increased, either rebounding naturally or through reintroduction and active management. (2) A group of open-land species was uncommon or absent at European settlement, increased greatly with forest clearance, peaked in the nineteenth or early twentieth century and has subsequently declined to low abundance. This group includes grassland, shrubland, and early successional species that are the current focus of intensive conservation efforts. Some of these species are common elsewhere, others are globally rare, and for many, records are inadequate to determine if they are native to New England. (3) A few animals were extirpated, including some that became globally extinct. Although small in number, some of these species were important ecologically or culturally in the New England landscape. (4) Numerous birds and at least two mammals have naturally expanded their ranges into Massachusetts, from northern, southern or western distributions. (5) Non-native species have been introduced purposefully or accidentally and some have become naturalized and abundant. (6) Finally, numerous persistent species have been present since settlement and have fluctuated in abundance, but have not displayed major directional changes.

Species declining with recent recovery

This rebounding group is varied but predominantly comprised of birds and moderate to large-sized mammals that depend on and use forested environments (Appendix 1). 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 3–10% annually, this group is the focus of research and management as well as frequent human conflict. Four of the more notable mammals are black bear, moose, beaver and white-tailed deer, whereas important bird species include great blue heron, bald eagle, osprey, pileated woodpecker, wild turkey, and raven.

Black bear are thriving across south-central to northern New England, and in Massachusetts they are well-established in a population of approximately 3000 individuals centred on the area west of the Connecticut River (Fig. 3; DFWELE, 1999b; Daily Hampshire Gazette, 2000, 2001; J. Cardoza unpubl. data). Although hunted to near extirpation in the nineteenth century save for a small population in the Berkshire mountains, bear thrived with reforestation and a reduction in hunting pressure (Cardoza, 1976). Currently the population is increasing at about 8–10% annually and is expanding eastward into more densely populated areas (DFWELE, 2000a). Bears are omnivores feeding extensively on mast (acorns and beechnuts), fruit, roots, and insects, supplemented by agricultural crops (e.g. corn and other vegetables) and backyard foods like birdseed and garbage. Increasing incursions into suburban areas have prompted many efforts at public awareness and education as well as an expanded hunting season in an attempt to slow the population growth. However, with fewer than 150 animals removed annually and public opinion generally opposed to greater hunting and trapping or tracking with dogs, the bear population will certainly continue to grow and expand geographically.

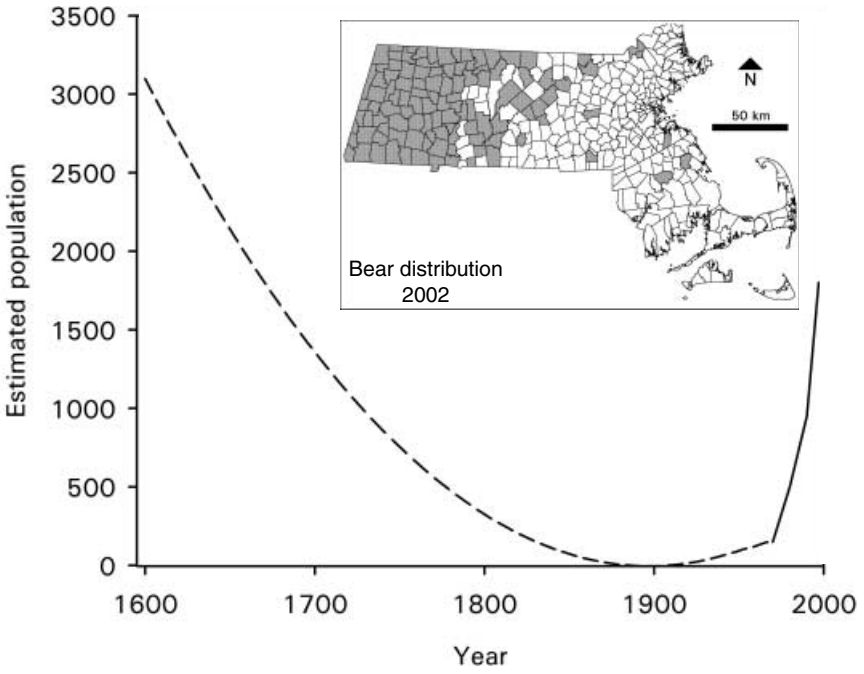

Figure 3 Current distribution and historical dynamics of the bear population in Massachusetts.

Although occasionally present in Massachusetts since the 1950s, moose have been established as a resident population for only slightly more than a decade (Vecellio *et al*., 1993; DFWELE, 1999a, 2000b). Centered on north-central and western Massachusetts because of population expansion from Maine, New Hampshire, and Vermont, moose are increasing rapidly (current estimates for the resident statewide population is 700 animals) and their presence is widely noted through heavy and selective browsing on woody and herbaceous plants. Moose may generate major local impacts on forest ecosystems ranging from changes in structure and composition to shifts in nutrient cycling (cf. Pastor *et al*., 1993; VT ANR, 2001). Because of their size, speed, nocturnal behaviour and seasonal mobility and aggressiveness, moose generate frequent human conflicts (Mirick, 1999). In 1998, ten people died in more than 1100 moose-car accidents across northern New England, although there have not yet been any fatalities in Massachusetts (DFWELE, 2000a, and unpubl. data). The region-wide increase in the moose population has led to progressive establishment of hunting seasons across Maine and northern Vermont and New Hampshire. In neighbouring Vermont, the population has grown from approximately 200 to more than 3000 in the last 20 years (VT ANR, 2001). In Massachusetts, moose are protected by a legal statute enacted in 1908, a fact that complicates management options.

Beaver (*Castor canadensis*) and white-tailed deer (*Odocoileus virginianus*) are important examples of rebounding species that decreased early in the historical period and have recently increased substantially. These two species are of particular interest because of their great influence on natural ecosystems and the significant management issues that they bring to the modern landscape (Figs 4 and 5; Naiman *et al*., 1988, 1994; Nelson, 1997). 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 (Bragdon, 1996). Both were also significant prey for large carnivores, including cougar, wolf, and humans.

Beaver were a focus of trapping and trading by the French, Dutch, and English in the early seventeenth century, including John Smith who returned to London from New England in 1616 with 1100 skins. By the late 1620s, Governor William Bradford of the Massachusetts Bay Colony reported shipments of over 12,500 pounds of beaver pelts to Britain. In Massachusetts, revenue from the beaver trade helped to finance settlement, encourage exploration, and generate friction among Indian groups. Ultimately the pelt trade led to the extirpation of beaver from south-eastern Massachusetts by 1635 and all but the northern Berkshires by 1700. As beaver declined in southern New England, 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.

Following more than a century's absence, efforts to re-introduce beaver in the late 1920s commenced with enactment of protective legislation and releases of animals from New York in western Massachusetts (Fig. 4). With

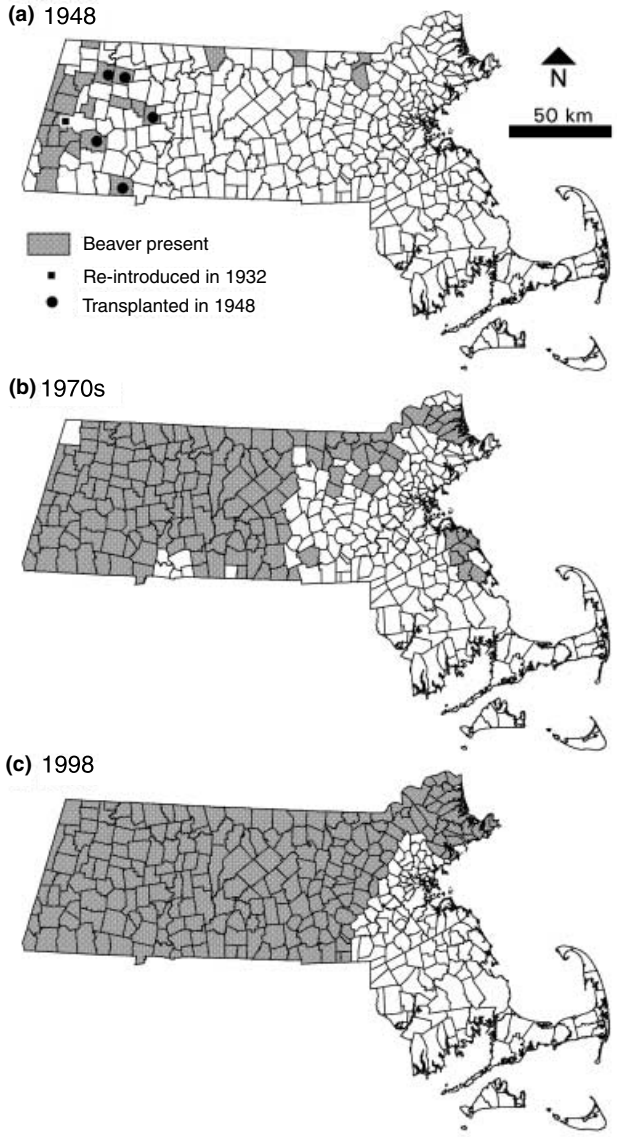

Figure 4 Modern expansion of the beaver population in Massachusetts following reintroductions in the 1930s and 1940s. By 2000 the statewide beaver population was estimated at 70,000 animals.

continued efforts the species expanded rapidly and naturally and by the late 1980s the Division of Fisheries and Wildlife indicated, 'beavers are…restored to all suitable habitats.' In New England's heavily wooded landscape, with its abundance of streams, wetlands, and lakes, beaver populations are thriving. The ecological impacts of the species are difficult to overstate. Through creation of dams, flooding of adjoining uplands, and selective browsing, beavers alter local hydrology and biogeochemistry, create wetlands, modify soils, flood and kill extensive forests, selectively alter vegetation composition, diversify landscape patterns, and create important new habitats (Francis *et al*., 1985; McMaster, 1989; Gurnell, 1998; Correll *et al*., 2000). The

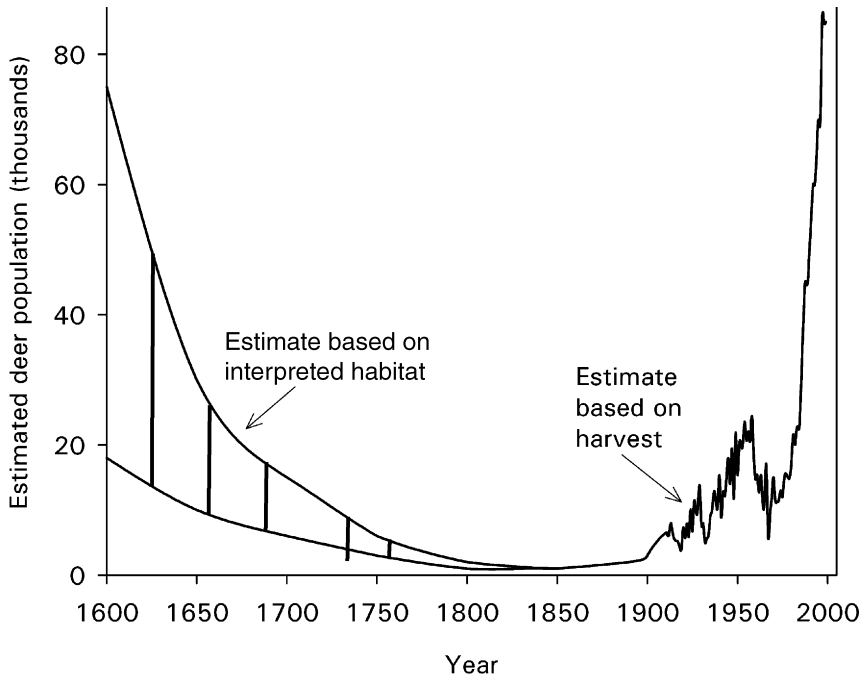

Figure 5 Historical changes in the population of white-tailed deer in Massachusetts. Two early scenarios are depicted that bracket the extreme high and low estimates at the time of European settlement.

indirect influence of beaver on other wildlife is equally important. The ponds, wetlands, dead trees, and forest openings offer unusual habitats in a landscape dominated by dense forest (Grover & Baldassarre, 1995).

However, many impacts of beaver, especially the elevation of local water-tables, damming of streams and mortality of trees, have significant human repercussions (Grabbe, 1999). Notably, highway, housing, and septic system conflicts with beavers have risen dramatically in recent years. In addition, beaver and other mammals are hosts to diseases like *Giardia lamblia*, a protozoan that causes human illness (Dazak *et al.*, 2000). Despite the fact that most, if not all, *Giardia* outbreaks in New England may be of human origin (e.g. from human waste fouling water supplies; J. Cardoza, unpubl.), the implication of beavers in *Giardia* outbreaks have prompted trapping, relocations, and public debate. Beaver currently have no significant predators in southern New England and the social environment of Massachusetts is inimical to trapping. A statewide referendum in 1996 led to a near total ban on leg-hold and body-gripping traps and a corresponding decline in harvest by trappers from 1136 beaver in 1996 to ninety-eight animals in 1998. With a beaver population estimated at approximately 70,000 (DFW unpubl. data) and complaints to wildlife agencies rising, there is a major challenge for the human population to grapple with how to coexist with this remarkable animal.

White-tailed deer underwent a similar trajectory as beaver, although they were never completely eliminated from Massachusetts and therefore did not require as intensive intervention to facilitate their recovery (Fig. 5; DeGraaf *et al.*, 1992; Hodgkins, 2000). Deer were important in Indian and early Colonial landscapes and economies, and their remains generally comprise the most abundant vertebrate fossil in archaeological sites (Allen, 1929; Bragdon, 1996). It is likely that Indians and the grey wolf were major predators as deer provided an important source of food, tool-making materials, and clothing (Kay, 1994). However, quantification of Indian impacts on deer is as fraught with uncertainty as population estimates of either species (cf. Hodgkins, 2000; Fig. 5). Intense hunting, coupled with land clearance by an expanding Colonial population, led to noticeable declines in deer and the promulgation of many early, and ultimately futile, attempts at hunting regulation. In 1698, Massachusetts began prohibiting deer hunting between January 15 and July 15, and enacted a 3-year moratorium on deer hunting in 1718 as declines continued. Deer 'reeves', one of the earliest attempts at game wardens in the US, were appointed in every town in 1739.

Through the late eighteenth and nineteenth centuries, deer became increasingly uncommon and were eventually extirpated across the central two-thirds of the state. Small populations persisted in Berkshire County in the west, and in the pine and oak woodlands near Cape Cod. A 10-year hunting moratorium in 1898, coupled with farm abandonment and a regional increase in shrubland and woodland, initiated a rebound in the population to an estimated level of 5000 by 1905. The growing population led to crop losses, illegal hunting, and the establishment of a regulated hunting season in 1910. Although the season has been modified repeatedly in attempts to control the size and demography of the herd, the population has continued to expand, particularly since the 1980s. Current estimates suggest a population of 90,000 animals, with 10,000 deer harvested by hunters annually and another 7000 killed by automobiles (DFW, unpubl. files). 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 (Brown *et al*., 2000; VT ANR, 2000a,b; McDonald *et al*., 2002).

The expanding deer population may exert a profound impact on forest ecosystems with selective deer browsing ultimately driving long-term changes in forest composition and structure (Whitney, 1984; Tilgham, 1989). However, these impacts will vary spatially because of the great heterogeneity in deer density. The consequences of such geographical variation in hunting and deer browsing are strikingly apparent in central Massachusetts. Active hunting throughout this broad area, including Harvard Forest lands, has maintained a low deer population that exerts little impact on forest regeneration (Cooper-Ellis *et al*., 1999). In contrast, a 55-year ban on hunting in the nearby 25,000-ha Quabbin Reservation led to a dense deer population and a severe decline of seedlings, saplings and understory (Dizard, 1999). Re-institution 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 US, 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 and infestation of the tick-borne Lyme disease (Barbour & Fish, 1993). As a consequence, the cultural perspective of deer is undergoing a remarkable shift in recent decades from noble and wild game animal to neighbourhood pest.

Six highly conspicuous large birds are included in the group of rebounding species (pileated woodpecker, wild turkey, raven, osprey, eagle and great blue heron; other species undoubtedly increasing include raptors like great horned and barred owls). Pileated woodpeckers, the region's largest woodpecker species (*c*. 30 cm tall), are dependent 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 (DeGraaf & Yamasaki, 2001). 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 over-hunting but has been actively reintroduced since the 1930s, with successful populations establishing especially in the 1970s (Cardoza, 1983, 1993, unpubl.). Turkey have increased across much of the state, reaching populations of nearly 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 in fall and spring seasons. Ravens, which closely resemble the smaller crow, are 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 road kill.

Osprey and eagle are large raptors whose populations were decimated by indiscriminate killing and antipathy towards raptors in the seventeenth to nineteenth century. These species were further affected by shell-thinning because of the bioaccumulation of 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 towards predators, ospreys are undergoing a remarkable rebound, from a low of less than fifty in the 1970s to more than 350 today (Delorey, 1999; VT ANR, 2000a). Although heavily concentrated in coastal areas, this species should continue to expand inland up the major river-ways and into the watersheds of large lakes. Eagles have been reintroduced through active hacking programmes 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 feather hunting and wetland and water quality deterioration. Now afforded protection, and with improved water quality, heron populations have rebounded (DHG, 1997). Further, the recent increase of beaver has exerted a profoundly positive impact 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 open land habitat favoured many native species that were uncommon in the forested landscape (Askins, 1993; Motzkin & Foster, 2002). This land cover transformation may also have enabled grassland and shrubland species from regions including the Midwest to immigrate to New England (Askins, 2000; Foster *et al*., 2002). Species including reptiles, amphibians, diverse birds and mammals like 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 (Fisher, 1933; Litvaitis, 1993, 2001; Porter & Hill, 1998; Braile, 2000). Although exhibiting diverse population trajectories according to their habitat preferences, e.g. 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 habitat becomes woody or is developed for human uses (McAuley & Clugston, 1998). As a consequence, this group includes some of the most vulnerable populations in the northeastern US (Norment, 2002).

In many ways the most dramatic and interesting example of a favourable response to historical land-use is provided by the grassland bird species, which are quite uncommon today (Figs 6 and 7). Indeed, the upland sandpiper, vesper sparrow, grasshopper sparrow, meadowlark, bobolink and savanna sparrow are a major focus of environmental concern that present a substantial management challenge and

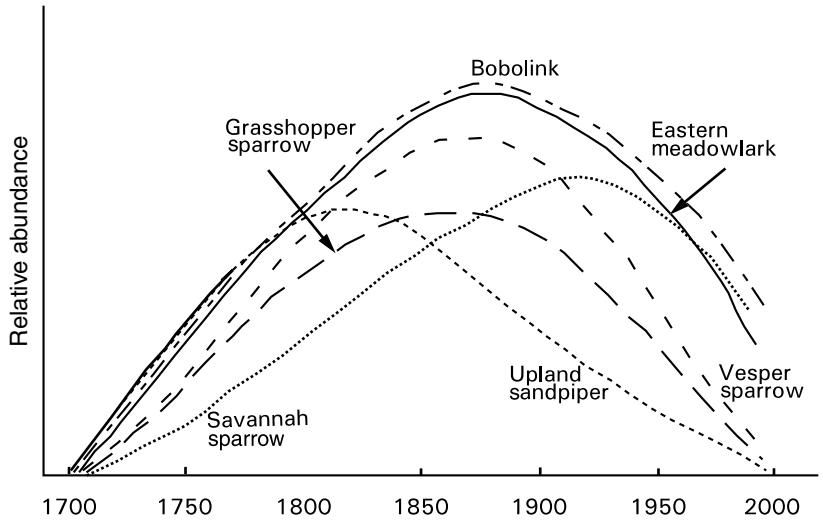

Figure 6 Relative changes in the population size of important grassland bird species in Massachusetts through time. Data from Massachusetts Division of Fisheries and Wildlife, and Jones & Vickery, 1997).

interesting ethical issue for conservationists (Jones & Vickery, 1997).

The early history of these birds is uncertain. Like most passerines and non-game species, they were not recorded until 1839 and the publication of Peabody's *A Report on the Ornithology of Massachusetts*, which was the first attempt at a comprehensive bird list. Consequently, their native status is uncertain. However, these birds proliferated in the agrarian landscape with the population growth and geography of individual species varying because of subtle differences in reproductive and foraging habitat. Through the height of agriculture (1830–1870) the upland sandpiper, which utilizes large grassy areas with low vegetation, was recorded by Nuttall and others as '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 (DeGraaf & Yamasaki, 2001). Vesper sparrows were so plentiful in open fields and upland pastures from Cape Cod to the Berkshires that Forbush (1925–29) considered it and the song sparrow the 'most abundant ground sparrow in Massachusetts.' The grasshopper sparrow, which utilizes large grasslands with patchy bare ground and few shrubs, apparently peaked slightly later in the late nineteenth century and was considered abundant across the landscape (Merriam, 1877) and found in 'spectacular abundance' on Cape Cod, Nantucket, and Martha's Vineyard. These trends were paralleled by more familiar birds of New England's agricultural past–such as the bobolink, meadowlark, northern bobwhite, and red-winged blackbird.

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 (Jones & Vickery, 1997; Askins, 2000). The upland sandpiper declined first, but by the mid-twentieth century the number of breeding sites for all grassland and heathland species greatly declined statewide (Motzkin & Foster, 2002). Currently the upland sandpiper is listed in Massachusetts as 'endangered', whereas vesper and grasshopper sparrows are 'threatened.

Ironically, ten of eleven most important refuges for these uncommon grassland species are industrial or military sites where populations are maintained through the efforts of managers and conservation agencies to regulate mowing and burning regimes and control disruptive human impacts. As a consequence of their uncertain native status and clear historical and modern dependence on cultural landscapes, these species are at the heart of the debate over openland management and importance (Motzkin & Foster, 2002). Although largely unknown by the general population, their remarkable historical dynamics, their imperilled status, their ability to capitalize rapidly on new habitat, and their current reliance on artificial habitats make them important examples of the fascinating interface between policy discussion and historical–ecological research.

Extirpated/extinct

The loss of wildlife species receives considerable attention as scientists seek to understand the factors associated with species' declines, and the effect that these exert on current ecosystem processes (Porter & Hill, 1998). 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 north-eastern US, relatively few species of plants or animals were driven extinct (cf. Wilcove, 1990; Wilcove, 2000). Arguably the two most important examples of colonial extinction from the temperate forests of New England are the passenger pigeon, which was widespread and abundant, and the less common and more locally distributed heath hen (see Gross, 1932; Wilcove, 1990; Motzkin & Foster, 2002).

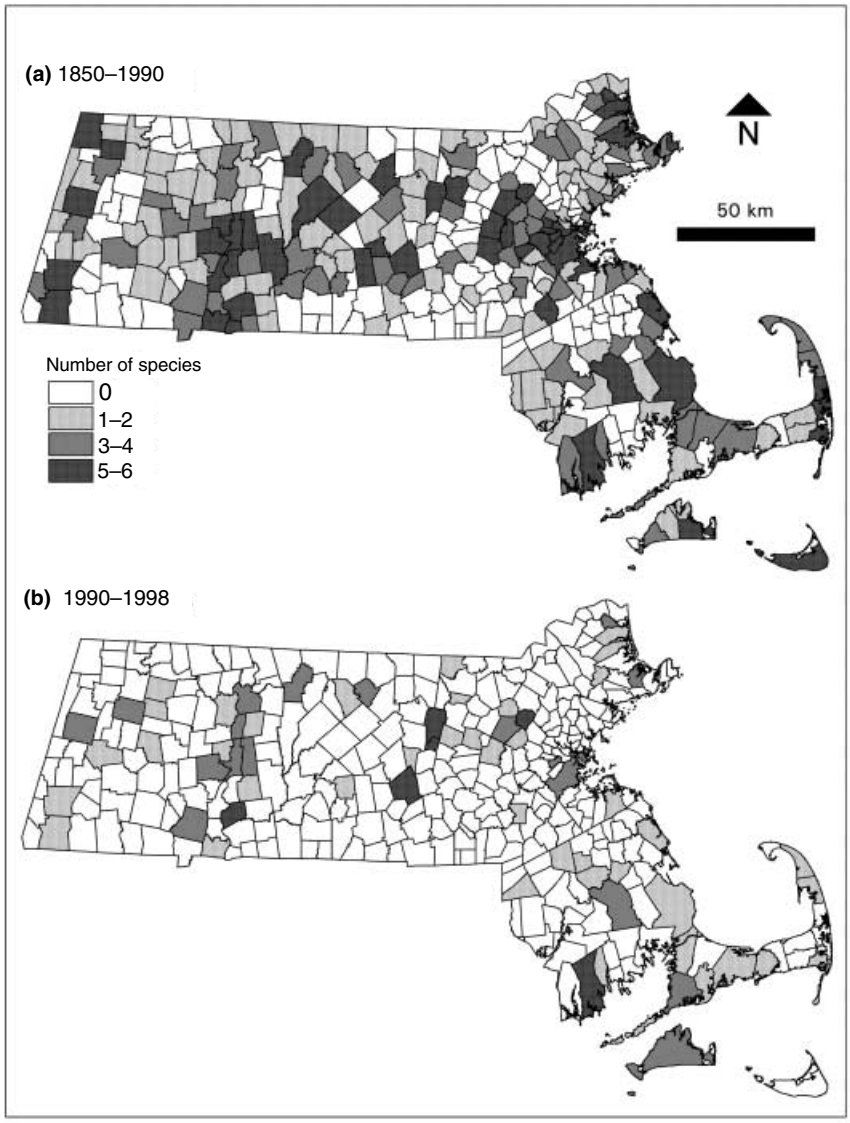

Figure 7 Historical changes in the relative abundance of important grassland bird species in Massachusetts. The six species include bobolink, eastern meadowlark, savanna sparrow, vesper sparrow, grasshopper sparrow and upland sandpiper. Data from Massachusetts Division of Fisheries and Wildlife, and Jones & Vickery, 1997).

In contrast, a relatively large group of species remains regionally extirpated, but represent potential candidates for reintroduction. Although some of these species such as wolverine and lynx were uncommon, 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 (Fig. 8). Large carnivores are under-represented in the modern landscape but might play a key role in controlling the populations of other species and thereby influencing forest conditions. Consequently, the ecological, management and cultural ramifications of their reintroduction are increasingly discussed (cf. Soule & Terborgh, 1999; Darling 2000; Berger *et al.*, 2001).

Wolves have large ranges but are habitat generalists that prefer areas with low human densities. Although their diet primarily consists of ungulates (e.g. deer, moose) along with 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 grey wolf was widespread and relatively abundant across New England (Fig. 8). However, a concerted effort to eliminate the species commenced almost immediately after settlement; this, combined with land cover changes and a decline in prey species, eliminated wolves on a broad scale. The Massachusetts Bay Colony established the first wolf bounty in 1630 and subsequent local bounties fuelled active extirpation. Between 1650 and 1655, bounties were paid on 147 wolves, increasing to a peak in the 1650s when over 1000 wolves were killed in Massachusetts in a 4-year span. From 1700 to 1737, 3043 bounties were paid. Intact populations appear to have been restricted to the Berkshires and Cape Cod by the mid 1700s. By the early 1800s, wolf killings were uncommon and many 'last sightings' were noted in town histories. A wolf that reputedly killed 3000 sheep near the base of Cape Cod was killed in the 1830s and may have been the last native wolf in

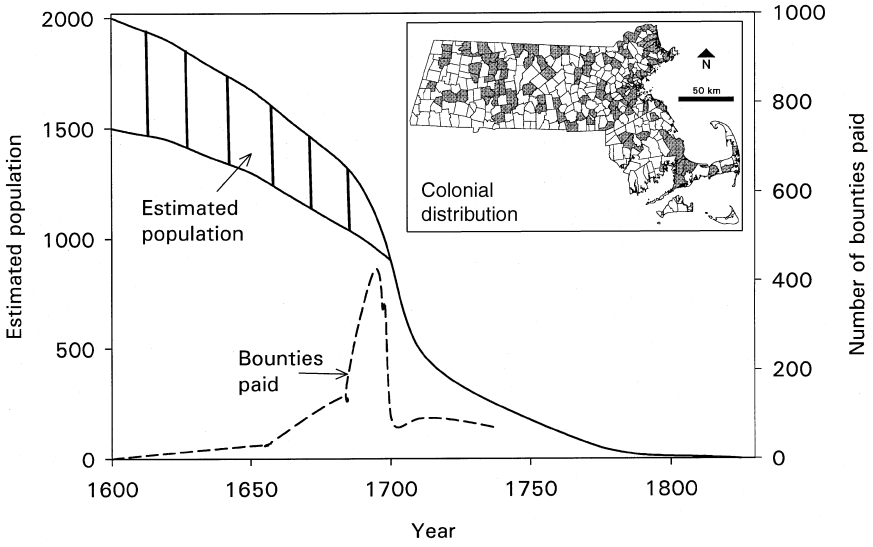

Figure 8 Colonial distribution and decline of the grey wolf in Massachusetts.

the state (Massachusetts Division of Fisheries and Wildlife, unpubl. data).

Natural range extension

Throughout the historical period, but increasingly in the twentieth century, wildlife species have naturally expanded their ranges into Massachusetts, including at least two mammals (eastern coyote and Virginia opossum) and many birds that have become abundant (e.g. turkey vulture, northern mockingbird, tufted titmouse, cardinal (cf. Cardoza, 1981; MNHESP, 1997; Thomas & Lennon, 1999; Wilson, 1999; Hodgkins, 2000; DeGraaf & Yamasaki, 2001; Malcolm *et al.*, 2001)). 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 climate change, availability of new food resources (e.g. winter bird seed and road kill), changes in competition and predation, and habitat and land cover change. Among these species, however, the coyote has embraced the most remarkable, continental-scale expansion, and exerts the greatest influence on forest ecosystems (Fig. 9).

Prior to European settlement coyotes ranged the western prairies from central Mexico to southern Canada. With changes in land use and the decline of the wolf, which is a predator and competitor, coyote began expanding significantly in the nineteenth century (Cardoza, 1981). It reached New York by the 1920s, New Hampshire and Maine by the 1930s, and Massachusetts by the late 1950s, when the first animals were shot (Rezendes, 1999). The Massachusetts population rapidly expanded in size and geographical area, reaching 500 by 1979, and a loosely estimated 3000–4000 in 1996 (J. McDonald, pers. comm.). Although a hunting and trapping season was initiated in 1981, the number of animals killed each year is relatively low and the species occupies the entire state including a few coastal islands and is continuing to increase.

Although the coyote represents the first large canine predator to roam the Massachusetts landscape in nearly three centuries, it does not completely replace the wolf ecologically. Eastern coyotes are larger and do have a greater tendency towards pack-like behaviour than their western counterpart. Nonetheless, they are smaller than wolves, are more adaptable to a range of habitats including human environments, and typically forage on smaller prey such as rodents, birds, amphibians and small mammals. Eastern coyotes do take deer, although the magnitude of this activity is uncertain. Nonetheless, 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

Through introductions, a wide range of organisms, from microbes to mammals, have been added to the state's biota (Appendix 1). Although the vast majority of introductions fail or have only local and transient impact, a few have generated widespread populations that have exerted major impacts on natural ecosystems (Orwig & Cobb, 2002; Paillet, 2002). The earliest introductions were accidental, including the house mouse and black rat, which have become common. A second group were game animals, primarily fish and birds, that were introduced to replace disappearing native species in intriguing attempts to fill what were perceived as vacant niches, or in an effort to provide novel hunting and fishing opportunities. Similarly, ring-necked pheasant, eastern cottontail, black-tailed jackrabbit, and European rabbit have maintained low to widespread populations as a consequence of intentional, and in some cases (e.g. pheasant), persistent human efforts. Ironically, the same public agencies that today attempt to restrict the introduction of exotic plant and animal pests were responsible for the active introduction and maintenance of many non-native game species. The

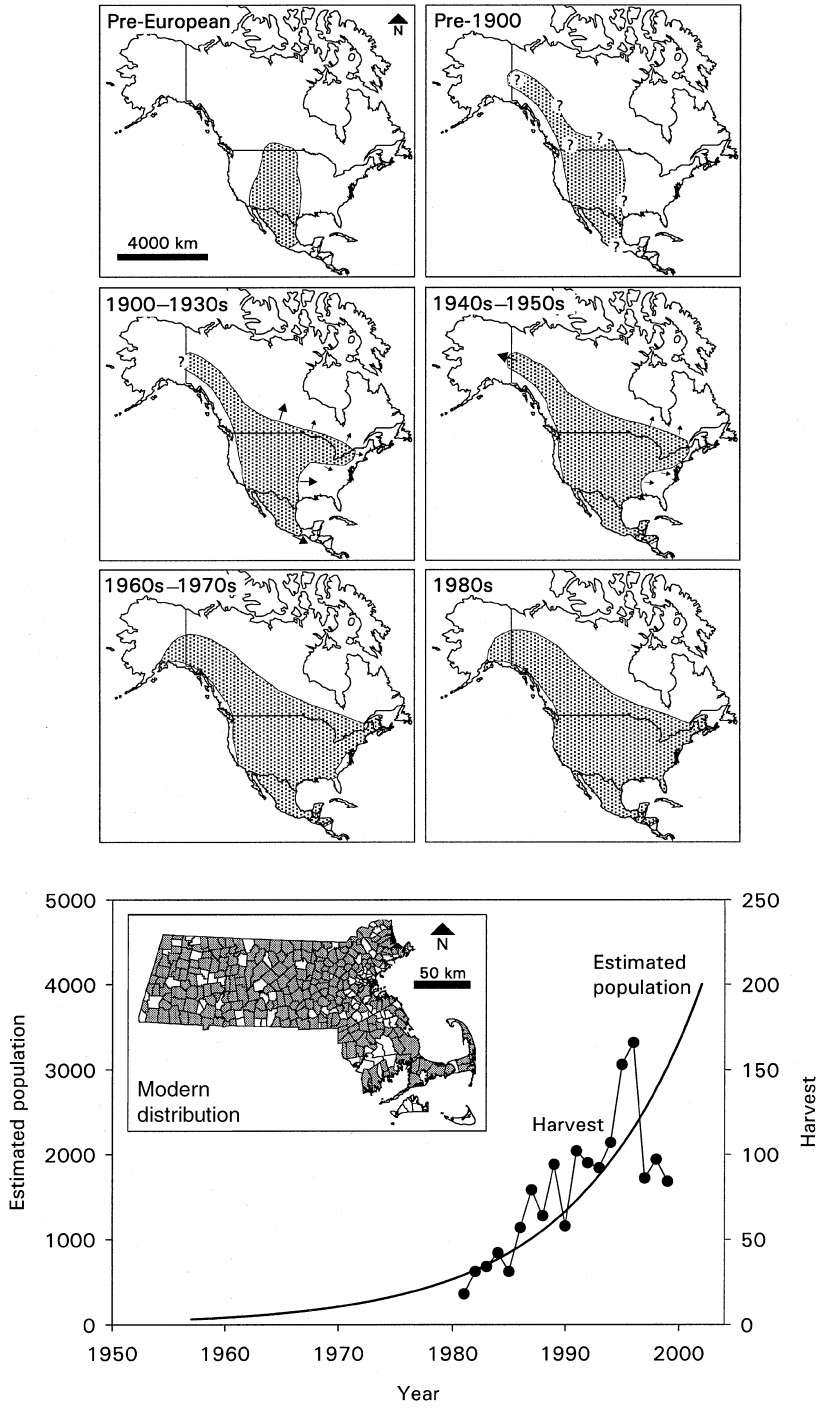

Figure 9 Range extension of the coyote and its local increase in population in Massachusetts. From Moore and Parker (1992) and J. Cardoza (unpubl. data).

ecological consequences of these introductions are poorly understood as research effort has been focused on successful establishment, rather than attendant impacts on habitat quality or native species.

Finally, numerous non-game 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 over 500,000 by the 1930s, but has subsequently declined somewhat, apparently because of winter mortality. Another common species, the house sparrow, was released in 1858 and introduced in 1868–69 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 (DeGraaf & Yamasaki, 2001).

Persistent species

In contrast to the long-term directional dynamics discussed above, numerous species have remained relatively common over the last 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 fisher, whereas bobcat populations have undoubtedly fluctuated with availability of prey, including rabbits (Hosley, 1937). Similarly, crows and grey 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 (Hornaday, 1913). Interestingly, the grey squirrel population dropped sharply between 1910 and 1920, evidently in response to the widespread mortality of chestnut trees that succumbed to the fungal 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 as abundant and widespread today as before the blight. Overall, these and many other species exhibit no major long-term trends.

DISCUSSION

Ecological implications and social consequences of wildlife dynamics

Clearly, wildlife populations have been dynamic in response to historical changes in landscape conditions and habitat availability, human persecution, and a range of other direct and indirect consequences of human activity (Hornaday, 1913; Matthieson, 1959). An understanding of these dynamics provides a useful background for policy decisions and affords interesting insights into the functioning of the New England landscape.

A basic question emerging at the community level for both plants and animals concerns the coherence of species assemblages through time (Faunmap, 1996). At the most fundamental level, ecologists are interested in whether assemblages of plant or animal species exhibit continuity through time or whether, in contrast, the species operate fairly independently of one another. Although natural history texts are replete with examples of tight relationships among specific pairs or suites of species (e.g. specialized plants and their animal pollinations; predator–prey cycles, etc.), the question remains whether such examples are representative of more general interrelationships or whether the majority of species actually form loose and highly malleable associations. Palaeoecological and archaeological studies of plants and animals indicate that through the post-glacial period, individual plant and animal taxa responded quite independently to the many different climatic and environmental changes and landscape settings that arose (Graham, 1992; Faunmap, 1996; Davis & Shaw, 2001). Necessarily, such individualistic behaviour produced a sequence of quite different assemblages of organisms through time as a series of unique environments unfolded. Thus, the lengthy, although taxonomically incomplete, post-glacial record indicates that the suites of species that we see in the landscape today are novel and have no great historical continuity (Faunmap, 1996).

The historical data on wildlife distributions and abundance confirm this pattern over a much shorter time period during which land cover and the human environment have changed substantially but physical environmental changes have been modest. Understandably, there are strong interactions among many species and many patterns of temporal change that may be generalized for groups of species. However, it is also clear that each species is unique in its dynamics; animal distributions and assemblages have changed continuously through time; and modern conditions and modern assemblages of organisms are distinct (cf. Wilcove, 2000). Few species exhibit closely linked dynamics, as each responded quite independently to the unusual combinations of habitat and human activity that the landscape experienced in the past 400 years. Although this individualistic behaviour is undoubtedly accentuated by the selective focus of humans on specific animals–either promoting or persecuting them in highly individualized fashion–it is apparent that the linkages among the organisms that we have examined are relatively loose.

The past changes and current composition of the region's fauna (and flora; cf. Bellemare *et al.*, 2002; Gerhardt & Foster, 2002; Motzkin *et al.*, 2002) are strongly influenced by human activity. Drawing this observation and the individualistic notion together, we can conclude that the seemingly natural appearance of the modern forest landscape, including its populations of coyotes, fishers, bears, moose, deer, and turkey, is culturally conditioned, even if not tightly directed, and is certainly only broadly analogous to presettlement conditions. Thus, the resurgence of many forest animal species with the reforesting of the landscape is quite distinct from a simple restoration of past conditions. Although perhaps obvious, recognition of the strong element of direct and indirect cultural control over modern landscape condition is critical for successful ecological understanding and conservation. 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 recent changes in wildlife populations, including the re-appearance of moose, fisher, and bear in much of New England, illustrate the sizable and important lags that may be inherent in ecological responses, given that suitable habitat has been available for many decades (cf. Malcolm *et al.*, 2001). Recognition of such lags also alerts us to anticipate many profound future changes, even in the absence of additional landscape change (Fig. 9). Forests, once established, take decades or centuries to mature; similarly, animals, even when highly mobile or reintroduced effectively, may require considerable time to migrate

and expand their populations, and to fill the existing or developing habitat (Cardoza, 1981). Examples like turkey, beaver, coyote and white-tailed deer illustrate this process and underscore the potential changes that await the moose, osprey, 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 last century, is undergoing additional alterations as the plants, animals and ecosystem processes slowly recover from or respond to changes in historical disturbance and habitats.

Indeed, the historical perspective underscores the fact that wildlife assemblages at any given time are comprised of species undergoing strikingly different trajectories (Fig. 2). Many animals that can thrive in the newly reforested and maturing forest landscape are well-established or expanding; some are just arriving, becoming established and are poised to flourish; and others are yet to arrive but may eventually appear 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 is an inevitable consequence of ongoing landscape and habitat changes. Therefore, in any particular historical sample, the assemblage of animals on the landscape includes diverse species, each of which is on a different ecological trajectory in response to past and ongoing changes: some are increasing, some declining, others are exhibiting few changes. In order for ecologists to evaluate species' roles and futures or for conservationists to develop effective management strategies, it is critical to be able to identify the specific trajectory associated with each species.

Ecologically, there remain many questions and challenges to our understanding of the consequences of the wildlife dynamics that we have highlighted (Foster, 2000). 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 some of the new species that have recently arrived such as coyote, but how do we evaluate the consequences of the absence of historically important species on the function 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 several 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 (Berger *et al*., 2001)? What effect will an expanding moose population exert on forest regeneration, understory composition and nutrient cycles? As we draw on palaeoecological 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.

Social consequences of wildlife dynamics

Awareness of the magnitude, rate and direction of wildlife dynamics provides useful perspectives for conservation and management. Based on past changes and trajectories, we can anticipate future declines in some species, major increases in others, and some of the potential dynamics and consequences of newly arriving species. At least two major and interrelated issues face wildlife managers. Foremost is that the trend towards a maturing forest landscape with large mammals, in conjunction with an expanding suburban and exurban human population, will lead to increasing conflicts between human interests and appreciation for wild nature. At the very least this raises the need for educating humans about wildlife, nature and its history and then using this education effectively to modify human behaviour and attitudes. In the case of many of the larger mammals (e.g. bear, moose, beaver, coyote), the social carrying capacity of the landscape (i.e. 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 behaviour would enable greater populations to be tolerated more safely. Secondly, as the modern fauna is dominated by relatively few, large species and lacks major predators, there is a need to more effectively regulate wildlife populations, either through direct management or through well-conceived re-introductions of additional species. This is a formidable task for a suburbanized 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 (Dazak *et al*., 2000). Beavers cut trees, flood cellars, roads, and sewer systems; deer and moose can alter forest composition, damage ornamental, horticultural and timber assets, and present a major hazard on highways; coyotes and bear may become too accustomed to people leading to potentially dangerous interactions; bear, deer, raccoons and other species may exert major damage to agricultural products; and a range of diseases from *Giardia* and Lyme disease to rabies and West Nile virus can be promoted or transmitted to humans and domesticated animals via animal vectors (Barbour & Fish, 1993; Tiedemann, 2000; Gompper, 2002). Current US expenditures to deal with Lyme disease alone are estimated to exceed $500 million per year (Dazak *et al*., 2000), and southern New England states like Connecticut experience as many as 75,000 cases of the disease annually (Walsh, 2000).

Evaluating the benefits and costs of wildlife and developing socially acceptable measures of control will be a major challenge for New England's future. Although it supplies few direct solutions, the evaluation of historical trends can assist in defining the issues, anticipating conflicts, and developing strategies for long-term changes. It 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.

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BIOSKETCHES

David Foster is an ecologist who investigates the long-term dynamics of primarily forested ecosystems changing as a consequence of natural disturbance, land-use practices, and environmental change. He is director of the Harvard Forest.

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Appendix 1 Historical dynamics of mammals and birds in Massachusetts and adjoining areas of New England. Compiled from DeGraaf & Yamasaki (2001), Massachusetts Department of Fisheries, Wildlife and Environmental Law Enforcement, and other sources

Regionally extirpated or extinct (+)		
Eastern grey wolf	Sea mink (+)	Great auk (+)
Elk	Cougar	Heath hen (+)
Indiana bat	Wolverine	Labrador duck (+)
Lynx	Woodland bison	Loggerhead shrike
Marten	Woodland caribou	Passenger pigeon (+)
Mountain lion		Bicknell's thrush
Open land and successional habitat (species generally declining)		
Northern harrier	Sedge wren	Golden-winged warbler
Northern bobwhite		Brown headed cowbird
Killdeer	Brown thrasher	Black-throated blue
Spotted sandpiper	Nashville warbler	warbler
American woodcock	Chestnut-sided warbler	Mourning warbler
Mourning dove	Prairie warbler	Savanna sparrow
Common nighthawk	Yellow-breasted chat	Grasshopper sparrow
Whip-poor-will	Eastern towhee	Bobolink
Least flycatcher	American tree sparrow	Eastern meadowlark
Horned lark	Field sparrow	
Purple martin	Indigo buntings	New England cottontail
Bank swallow	Red-winged blackbird	Red fox
Barn swallow	Veery	Woodchuck
Ruffed grouse	Upland sandpiper	
Eastern Phoebe	Vesper sparrow	
Baltimore oriole	Magnolia warbler	
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		
Range expansion		
Northward or eastward		
Little blue heron	Northern rough-winged	Golden-winged warbler
Glossy ibis	swallow	Nashville warbler
Turkey vulture	Tufted titmouse	Worm-eating warbler
Black vulture	Carolina wren	Northern waterthrush
Mourning dove	Blue-grey gnatcatcher	Louisiana waterthrush
Barn owl	Northern mockingbird	Northern cardinal
Red-bellied woodpecker	Blue-winged warbler	
Acadian flycatcher	Cerulean warbler	Virginia opossum
Southward		Coyote
Herring gull	Bohemian waxwing	Rusty blackbirds
Great black-backed gull	Magnolia warbler	Purple finch
Golden-crowned kinglet	Swamp sparrow	
Hermit thrush	White-throated sparrow	
Persistent and 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

Appendix 1 *continued*

American robin		Raccoon
Yellow-rumped warbler	Bobcat	Red squirrel
Ovenbird	Eastern chipmunk	
Increasing recently		
Woodland species		
	Tree swallow	Beaver
Wood duck	Brown creeper	Black bear
Hooded merganser	Wood thrush	Fisher
Northern goshawk	Worm-eating warbler	Gray fox
Red-tailed hawk	Scarlet tanager	Moose
Broad-winged hawk	Red-headed woodpecker	White-tailed deer
Blue-headed vireo	Wood duck	
Great horned owl	Wild turkey	
Barred owl		
Pileated woodpecker		
Others		
Great blue heron		
Snowy egret		
Great egret	River otter	
Canada goose		
Mallard		
House wren		
Evening grosbeak		