Top Carnivores in the Suburbs? Ecological and Conservation Issues Raised by Colonization of Northeastern North America by Coyotes

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ust a handful of individual members of a population of top predators—wolves and tigers, orcas, and great white sharks, for example-hold the potential to disproportionately influence animal and plant communities. The importance of this phenomenon, known as a "top-down" effect, has been demonstrated in several recent studies. For example, as few as four killer whales may be responsible for a shift in 800 kilometers of Alaskan near-shore community structure, from a structure dominated by kelp forests with few herbivores to one with high numbers of sea urchins and low kelp densities (Estes et al. 1998). Similarly, just two or three wolf packs indirectly control tree community organization by regulating moose numbers in 544-km² Isle Royale, Michigan (Post et al. 1999). In coastal southern California, the presence or absence of coyotes in patches of sage-scrub habitat directly controls the distribution and abundance of smaller carnivores, which in turn alter scrub-breeding bird communities (Crooks and Soulé 1999).

Today in northeastern North America, the top terrestrial predator is the coyote, *Canis latrans*, an immigrant to the region that is anything but rare. Historically, the species was unknown to European settlers of eastern North America, who were more concerned with the presence of wolves and cougars. Coyotes were a predator of the Great Plains. Lewis and Clark didn't catch their first glimpse of a coyote until 1804, when they reached the eastern edge of present-day Nebraska (Ambrose 1996). Times have changed. Over the past two centuries the coyote has dramatically expanded its geographical range and is now ubiquitous throughout northeastern North AmerTHE EXPANSION OF THE COYOTE'S GEOGRAPHICAL RANGE MAY BROADLY INFLUENCE COMMUNITY STRUCTURE, AND RISING COYOTE DENSITIES IN THE SUBURBS MAY ALTER HOW THE GENERAL PUBLIC VIEWS WILDLIFE

ica (Figure 1; Parker 1995, Gompper 2002). It has even colonized seemingly isolated geographical regions such as Cape Cod and the Elizabeth Islands of Massachusetts, Cape Breton Island, Prince Edward Island, and Newfoundland of Atlantic Canada, as well as urban habitats such as parts of New York City. The culmination of this range expansion may arguably be the capture of a wild coyote in Central Park in the heart of Manhattan in 1999 (Martin 1999).

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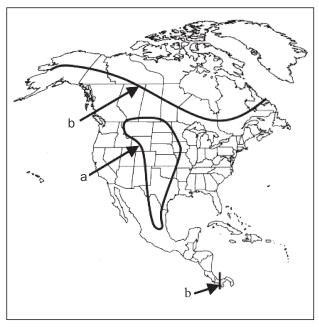


Figure 1. Geographic range of the coyote, Canis latrans. a. The approximate range of the coyote through the early 1800s was limited before European settlement of eastcentral North America dramatically altered landscape structure and carnivore community composition. b. The approximate current northern and southern limits of the range of the coyote encompass almost the entire Northern Hemisphere.

What has allowed this enormous range expansion? The flora, fauna, and landscape of the Northeast differ from that of centuries past, and two synergistic factors likely catalyzed the movement of coyotes into the region. First, the eradication of the gray wolf (Canis lupus) from its former range may have reduced the competitive pressures limiting coyotes to midwestern and western North America (Thurber and Peterson 1991, Peterson 1996). Second, humans may have altered the landscape and community structure by intensive logging and agricultural development, opening additional habitat to coyotes (Larivière and Crête 1992, Parker 1995). This landscape conversion also favored white-tailed deer, and both species have expanded their range northward to the limits imposed by snow cover and resource availability (Parker 1995). Whatever the reason for this range expansion, it is clear that humans throughout the Northeast are now confronted with issues that have not existed in many parts of the region for more than 100 years-how to deal with the presence of a carnivore that is perceived by some segments of the public as potentially dangerous, and how to gauge the ecological and conservation effects of such a species in the region. While we know a great deal about the biology of coyotes, much of this knowledge comes from research conducted in western North America. It is unclear how transferable these findings are to the very different environment of the Northeast (Ray 2000).

Why focus on the Northeast? After all, coyotes are now found along the entire eastern seaboard, south into Mexico

and Central America, and north to Alaska. There are several reasons. Coyotes have been in the Northeast longer than in the Southeast, where they did not arrive until the 1960s (Parker 1995), and coyotes in the Northeast have been the subject of more scientific study than in other areas of recent expansion. In addition, coyotes are not the apex predators in Alaska and Latin America, where mountain lions, jaguars, wolves, wolverines, and grizzly bears live. In the Northeast, coyotes very likely dominate all other predators except adult black bears. Coyotes in the Northeast have also received attention in the media and scientific literature because

- They are perceived as being physically larger than coyotes from elsewhere in their range.
- Attacks on humans seem to have increased in the Northeast.
- It has been suggested that genetic introgression from wolves has occurred and that coyotes may be filling the ecological niche of wolves in the region.
- Their diet is more reliant on ungulates than in other parts of their expanded range.
- The population resulted from a colonizing wave different from that for the southeastern population.

These issues suggest the need to evaluate the changes that have happened or are likely to occur in the future as a result of the expansion of coyotes into the Northeast. This article outlines some of the ecological, conservation, and policy issues to be faced.

The ecological relevance of coyotes

Coyotes are competitors with, and predators of, a wide array of species. How might coyotes in the Northeast influence the distribution and abundance of other species, including those of conservation concern? As a large carnivore, its potential for top-down influences on a broad array of organisms is great. Critical to understanding how coyotes alter community structure may be our ability to assess the effects of coyotes on other carnivores. Just as wolves in some regions limit coyotes by interference competition, coyotes limit smaller carnivores (Harrison et al. 1989, Johnson et al. 1996). If the increase in covotes influences the population dynamics of other carnivores, a cascade of ecosystem effects may occur. For instance, the absence of coyotes in habitat fragments in southern California may result in "mesopredator release"-a sharp increase in the numbers of midsize predators-and altered bird communities (Crooks and Soulé 1999). Similar findings involving coyotes have been made elsewhere in North America, revealing indirect effects on waterfowl, songbirds, and rodents (Sovada et al. 1995, Rogers and Caro 1998, Henke and Bryant 1999). Studies of this sort are currently unavailable in the Northeast, which makes conclusions on the possible causes and effects of ecosystem change speculative. Nonetheless, ample empirical data support the occurrence of mesopredator release, and given the diverse mesopredator community (Ray 2000), it is reasonable to assume that such a release would also occur in the Northeast.

While evidence of a mesopredator release and its indirect effects in the Northeast may be lacking, the competitive dynamic that several of these species have with coyotes has been documented. Coyotes are generalist predators and can attain high densities relative to more specialized carnivores; the latter may decline because of exploitation competition. For instance, bobcat and coyote numbers may be inversely correlated because of resource competition (Litvaitis and Harrison 1989, Fox 1990). Similar concerns have been raised for coyote interactions with lynx, which was recently listed as a threatened species (USFWS 2000a).

Also, perceptions exist that coyotes are larger in the Northeast than elsewhere in their range, perhaps because of the belief that hybridization with wolves has occurred (Wilson et al. 1999), and that the animals may have assumed the ecological role of wolves in the region. Although data that support these perceptions are somewhat ambiguous (Parker 1995, Gompper 2002), these perceptions deserve further consideration, as wolves in particular have been shown to have dramatic effects on ecosystem structure (Post et al. 1999). The covote-wolf relationship in the Northeast-be it in a theoretical framework or based on fieldwork in northeastern Canada where the two species are sympatric—also deserves attention. Given that wolf recolonization or humanaugmented reintroduction into the northeastern United States is increasingly contemplated (USFWS 2000b), successfully predicting the interaction of coyotes and wolves will be a critical factor in the establishment of a viable northeastern wolf population, if such a reintroduction occurs.

Coyotes can significantly affect prey populations, especially if the latter are small or isolated (e.g., Crête and Desrosiers 1995). Of broader relevance, however, is not the risk of extirpating already reduced prey populations but rather the influence that predation by coyotes might have on robust populations, in particular, white-tailed deer, which are an important prey species for coyotes throughout the Northeast (Parker 1995, Gompper 2002). While a reduction in deer numbers might be welcomed in some suburban areas, coyotes and humans compete for ungulate prey in many parts of the rural Northeast, so the dietary habits of coyotes may be perceived as having direct economic impacts—both for the individual hunter and for industries and communities that depend on revenues associated with hunting (Sage 2001).

In this context, the underlying questions faced by wildlife managers and conservationists are twofold. First, do coyotes kill prey that would otherwise die from such causes as limited food availability or severe weather (compensatory mortality), or is mortality from coyotes additional to these other sources (additive mortality)? That is, does mortality caused by coyotes simply substitute for some other cause of mortality and thus have no broad effect on ungulate numbers or population dynamics (Bartmann et al. 1992)? Second, if coyotecaused mortality is additive, is the ungulate population of interest regulated by coyotes (which implies density-dependent predation), or are predation levels maintained over a range of prey densities (density-independent predation)? The former scenario would imply a shift in prey numbers to a new equilibrium, while the latter would mean that coyotes may be responsible for prey declines. Thus, when a prey population decreases because of disease, harsh winters, or overhunting, predation by coyotes could slow prey population recovery. Answers to these questions will be difficult to obtain, as the importance of coyotes will most likely be site specific, will depend on how human-caused mortality is considered in the equation, and may differ depending on whether prey density is measured to focus on total population size or on specific age classes, such as adults (Whitlaw et al. 1998, Dumont et al. 2000).

Far from always being an undesirable menace to the status quo, robust coyote populations may offer wildlife managers a novel tool, albeit a difficult one to control, for manipulating wildlife. For example, by reducing numbers of some mesocarnivores, the presence of a few coyotes may allow for dramatic increases in waterfowl, songbird, and game bird populations (Sovada et al. 1995, Rogers and Caro 1998). In addition, several vertebrates are threatened with local or regional extinction in the Northeast from mesocarnivore release. The Allegheny woodrat (Neotoma magister) is threatened regionally by the raccoon roundworm (Baylisascaris procyonis), whose definitive host has increased in recent decades (Balcom and Yahner 1996). The ability of coyotes to limit mesocarnivore densities could offer opportunities for mediating this type of conflict. The preference that coyotes show for white-tailed deer might also be welcomed in areas such as the suburbs, where hunting pressures alone are no longer sufficient to keep deer populations at a level acceptable to a public that increasingly views deer as pests. One could speculate that by altering the distribution and density of whitetailed deer, coyotes may also come to play an important role in lowering cases of tick-borne Lyme disease, for which deer play a critical role in the Northeast (Van Buskirk and Ostfeld 1995, Wilson and Childs 1997). These utilitarian benefits of a healthy top-predator population may reduce the need for controversial population control measures of species that are viewed by some as charismatic and by others as a nuisance.

The human factor

Colonization of northeastern North America by coyotes is not simply an issue for ecologists to ponder. For better or worse, interactions between coyotes and humans will increase, resulting in greater public scrutiny of wildlife management practices and an increased call for information on coyote populations. How issues concerning the loss of livestock and domestic animals to coyote predation, which many perceive to be unique to western North America, will play out in the Northeast remains to be seen. The real and perceived losses caused by predators are economically significant in western North America, raising genuine concerns about the protection and economics of livestock and farm animal production in the Northeast. At extreme levels, predation on domestic animals by coyotes may result in pressure from the public to increase programs to control predators (Kellert 1985).

Attacks on domestic animals also intensify fears of coyotes attacking humans. Attacks on humans are not unusual in the western United States, although death from these attacks is extremely rare. In some areas, attacks have recently increased in frequency (Baker and Timm 1998), and several have occurred in the Northeast (Gompper 2002). As coyote numbers increase in highly populated northeastern areas, attacks by coyotes on humans are also likely to increase. While the per capita risk of an attack is negligible, those attacks that do occur will very likely receive intense publicity, especially when they take place in suburban regions. This was the case for an attack in Cape Cod, Massachusetts, in 1998. Unfortunately, state and provincial agencies are sending differing, and sometimes contradictory, messages about the threat that coyotes

Table 1. Information given by state and provincial wildlife agencies about the threat of coyotes to humans and domestic animals. Information was collected from agency Web sites in January 2001. Note that the variability in the depth of the information given may relate to ecological factors such as the time of colonization of the region and the size of the coyote population, as well as to responsibilities and jurisdiction of the respective agencies—for example, whether the agency deals with livestock and wildlife damage control issues.

State or province	Agency	Information on Web site
Connecticut	Department of Environmental Protection—Wildlife Division	Detailed discussion of perceived threats to humans, livestock, and pets
Maine	Department of Inland Fisheries and Wildlife	None
Massachusetts	Department of Fisheries, Wildlife and Environmental Law Enforcement	Posting of a 9 August 1998 press release following an attack on a three-year-old Cape Cod boy, with detailed information for minimizing conflicts between coyotes and people or pets
New Brunswick	Department of Natural Resources and Energy—Fish and Wildlife Branch	Discussion of threats to livestock
Newfoundland and Labrador	Department of Forest Resources and Agrifoods—Inland Fish and Wildlife Division	None
New Hampshire	Fish and Game Department	Discussion of risks to livestock and pets. Information for humans: "As for your safety, coyotes pose little risk to people. In New Hampshire, there has never been a report of a coyote attacking a person."
New Jersey	Division of Fish, Game, and Wildlife	None
New York	Department of Environmental Conservation	Detailed discussion of perceived threats to humans and pets
Nova Scotia	Department of Natural Resources	Posted 6 October 1998, discussion of threats to pets, livestock, and humans, with this statement: "The very few cases on record are associated with coyotes that have lost their fear as a result of being fed by humans. An attack on a child in Cape Breton Highlands National Park last summer (1988) was by a young coyote accustomed to handouts."
Pennsylvania	Game Commission	Discussion of risk to humans, livestock, and pets, with this statement: "There have been a few incidents in the north- eastern United States where coyotes have attacked people. Why is unclear, but those who study these animals believe the coyotes mistook the persons attacked as wildlife prey."
Québec	Société de la faune et des parcs du Québec	None
Rhode Island	Department of Environmental Management	Discussion of risk to humans and pets. Posting of a 4 August 1998 news release that mentions that "attacks on humans are extremely rare—the only confirmed Rhode Island coyote bite was the result of an attempt to hand-feed the animal."
Vermont	Department of Fish and Wildlife	Brief mention of risk to pets. No mention of perceived threat to humans

may pose to humans and domestic animals (Table 1). Coyotes do occasionally attack humans, and wildlife agencies should not promote a message declaring that coyotes are harmless. Rather, agencies should recommend that people change their behavior to avoid problematic encounters with coyotes.

A problem in sending this message, however, is that our understanding of the ecology of coyotes in suburban environments is poor, thus making it difficult to predict how coyotes may behave in these areas. Most studies of coyotes in the Northeast have been conducted in rural, forested regions. The ecology of coyote populations that inhabit areas with higher human densities, such as suburban and coastal regions, is only now coming under study. For instance, recent research on Cape Cod revealed that coyotes were very adept at using habitats with relatively high (200–560 per km²) human densities (Way 2000). But we currently have no insight into such questions as how coyotes respond to the presence of humans, how coyotes interact with domestic cats and dogs, and how coyotes establish their foraging patterns in suburban environments.

Fear of attacks by coyotes on people and domestic animals and competition between human recreational hunters and coyotes for prey such as deer have resulted in calls for predator control and expanded hunting seasons on coyotes (Parker 1995). Coyotes may be density-dependent breeders, however, and dispersal varies as a function of control intensity. Thus, a successful coyote population control program must cover relatively large geographical regions and be continuously sustained. Otherwise, the success of a control program may be temporary, at best, and at worst will have no effect or may even stimulate population growth (Knowlton et al. 1999). The present political climate and the high population density of both people and domestic carnivores make the enactment of large-scale coyote control programs in the Northeast unlikely.

If people form their opinions about the value of carnivore conservation programs based on their personal dealings with carnivores, then one might speculate that negative interactions between humans and coyotes in the Northeast could decrease support for programs such as lynx recovery or wolf reintroduction. Northeastern coyotes are commonly implicated, rightly or not, for contributing to the low density of deer in parts of the Northeast and for filling the ecological niche of wolves, perhaps for even behaving more like wolves than coyotes (Sage 2001). These perceptions influence the views of stakeholders and the rural public on the need for wolf reintroduction efforts and on the possible impact of any reintroduced wolf population on prey species (Fascione and Kendrot 2001, Sage 2001). Thus, while coyotes are by no means threatened with extinction, they are very much a conservation issue in the Northeast and should be treated as such.

So what should be done? First, realize that the presence of coyotes in the Northeast represents a natural range expansion of the species, not an exotic invasion, and that the species is here to stay. Since coyotes do represent a threat to the public—albeit a very minor one compared with the damage inflicted by domestic dogs—state wildlife agencies should abandon the message that these animals are harmless. Instead, these agencies should continually reinforce the message that people should change their behavior to avoid problematic encounters with coyotes. Although most state wildlife agencies in the Northeast promote this message, a few still state that coyotes are harmless. Second, realize that the coyote represents to wildlife managers a possible opportunity in some areas to reduce the need for controversial and expensive management decisions. And finally, ecologists should realize that the presence of the coyote is an important conservation issue. The arrival of this generalist top predator is likely to dramatically influence animal and plant communities in coming years. The coyote's presence may also influence public opinions on the value of free-ranging large predators.

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References cited

- Ambrose SE. 1996. Undaunted Courage: Meriwether Lewis, Thomas Jefferson, and the Opening of the American West. New York: Simon & Schuster.
- Baker RO, Timm RM. 1998. Management of conflicts between urban coyotes and humans in southern California. Pages 299–312 in Baker RO, Crabb AC, eds. Proceedings of the 18th Vertebrate Pest Conference; 2–5 March; Davis, CA.
- Balcom BJ, Yahner RH. 1996. Microhabitat and landscape characteristics associated with the threatened Allegheny woodrat. Conservation Biology 10: 515–525.
- Bartmann RM, White GC, Carpenter LH. 1992. Compensatory mortality in a Colorado mule deer population. Wildlife Monographs 121: 1–39.
- Crête M, Desrosiers A. 1995. Range expansion of coyotes, *Canis latrans*, threatens a remnant herd of caribou, *Rangifer tarandus*, in southeastern Québec. Canadian Field-Naturalist 109: 227–235.
- Crooks KR, Soulé ME. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400: 563–566.
- Dumont A, Crête M, Ouellet J-P, Huot J, Lamoureux J. 2000. Population dynamics of northern white-tailed deer during mild winters: Evidence of regulation by food competition. Canadian Journal of Zoology 78: 764–776.
- Estes JA, Tinker MT, Williams TM, Doak DF. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science 282: 473–476.
- Fascione N, Kendrot SR. 2001. Facilitating citizen participation in Adirondack wolf recovery. Pages 51–59 in Sharpe VA, Norton B, Donnelley S, eds. Wolves and Human Communities: Biology, Politics, and Ethics. Washington (DC): Island Press.
- Fox LB. 1990. Ecology and population biology of the bobcat (*Felis rufus*) in New York. PhD dissertation. State University of New York, College of Environmental Science and Forestry, Syracuse, NY.
- Gompper ME. 2002. The ecology of coyotes in northeastern North America: Current knowledge and priorities for future research. Wildlife Conservation Society Working Paper. Forthcoming.
- Harrison DJ, Bissionette JA, Sherburne JA. 1989. Spatial relationships between coyotes and red foxes in eastern Maine. Journal of Wildlife Management 53: 181–185.
- Henke SE, Bryant FC. 1999. Effect of coyote removal on the faunal community in western Texas. Journal of Wildlife Management 63: 1066–1081.

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- Johnson WE, Fuller TK, Franklin WL. 1996. Sympatry in canids: A review and assessment. Pages 189–218 in Gittleman JL, ed. Carnivore Behavior, Ecology, and Evolution. Ithaca (NY): Cornell University Press.
- Kellert SR. 1985. Public perceptions of predators, particularly the wolf and the coyote. Biological Conservation 31: 167–189.
- Knowlton FF, Gese EM, Jaeger MM. 1999. Coyote depredation control: An interface between biology and management. Journal of Range Management 52: 398–412.
- Larivière S, Crête M. 1992. Causes et conséquences de la colonisation du Québec par le coyote. Québec: Ministère du Loisir, de la Chasse et de la Pêche, Direction générale de la faune. SP-1935.
- Litvaitis JA, Harrison DJ. 1989. Bobcat-coyote niche relationships during a period of coyote population increase. Canadian Journal of Zoology 67: 1180–1188.
- Martin D. 1999. Unleashed coyote captured in Central Park. New York Times, 2 April.
- Parker GR. 1995. Eastern Coyote. Halifax (Canada): Nimbus Publishing.
- Peterson RO. 1996. Wolves as intraspecific competitors of canid ecology. Pages 315–323 in Carbyn LN, Fritts SH, Seip D, eds. Wolves in a Changing World. Edmonton (Canada): Canadian Circumpolar Institute, University of Alberta.
- Post E, Peterson RO, Stenseth NC, McLaren BE. 1999. Ecosystem consequences of wolf behavioural response to climate. Nature 401: 905–907.
- Ray JC. 2000. Mesocarnivores of northeastern North America: Status and conservation issues. Wildlife Conservation Society Working Paper 15: 1–82.
- Rogers CM, Caro MJ. 1998. Song sparrows, top carnivores and nest predation: A test of the mesopredator release hypothesis. Oecologia 116: 227–233.
- Sage RW Jr. 2001. Wolves in the Adirondacks? Perspectives from the heart of the Adirondack Park. Pages 39–46 in Sharpe VA, Norton B, Donnelley S, eds. Wolves and Human Communities: Biology, Politics, and Ethics. Washington (DC): Island Press.

- Sovada MA, Sargeant AB, Grier JW. 1995. Differential effects of coyotes and red foxes on duck nest success. Journal of Wildlife Management 59: 1–9.
- Thurber J, Peterson RO. 1991. Changes in body size associated with range expansion in the coyote (*Canis latrans*). Journal of Mammalogy 72: 750–755.
- [USFWS] US Fish and Wildlife Service. 2000a. Determination of threatened status for the contiguous US distinct population segment of the Canada lynx and related rule: Final rule. Federal Register 65: 16052–16086.
- . 2000b. Proposal to reclassify and remove the gray wolf from the list of endangered and threatened wildlife in portions of the conterminous United States: Proposal to establish three special regulations for threatened gray wolves: Proposed rule. Federal Register 65: 43450–43496.
- Van Buskirk J, Ostfeld RS. 1995. Controlling Lyme disease by modifying the density and species composition of tick hosts. Ecological Applications 5: 1133–1140.
- Way JG. 2000. Ecology of Cape Cod coyotes (*Canis latrans var.*). MS thesis. University of Connecticut, Storrs, CT.
- Whitlaw HA, Ballard WB, Sabine DL, Young SJ, Jenkins RA, Forbes GJ. 1998. Survival and cause-specific mortality rates of adult white-tailed deer in New Brunswick. Journal of Wildlife Management 62: 1335–1341.
- Wilson ML, Childs JE. 1997. Vertebrate abundance and the epidemiology of zoonotic diseases. Pages 224–248 in McShea WJ, Underwood HB, Rappole JH, eds. The Science of Overabundance. Washington (DC): Smithsonian Institution Press.
- Wilson PJ, Grewal S, Chambers RC, White BN. 1999. Genetic characterization and taxonomic description of New York canids. Pages 8–15 in Paquet PC, Strittholt JR, Staus NL, eds. Wolf Reintroduction Feasibility in the Adirondack Park: Report to the Adirondack Park Citizens Action Committee and Defenders of Wildlife. Corvallis (OR): Conservation Biology Institute.