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THE ECOLOGY OF NORTHEAST COYOTES

Current Knowledge and Priorities for Future Research

By Matthew E. Gompper

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By Matthew E. Gompper



This summary report and working paper was prepared for the Wildlife Conservation Society by Matthew E. Gompper
Department of Fisheries and Wildlife Sciences
University of Missouri
Columbia, MO 65211
Email: gompper@missouri.edu

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Wildlife Conservation Society
International Conservation
2300 Southern Boulevard
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t: 718.220.1442
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SUMMARY

When Europeans first settled North America, wolves and puma dominated the large-predator community of the eastern deciduous forests. The coyote was a resident of the Great Plains and western North America and was unknown to settlers of the east. These days, puma are virtually extirpated east of the Mississippi, and aside from a handful of red wolves reintroduced in the southeastern United States and possibly an occasional transient gray wolf in the Northeast, wolves are also effectively absent. In contrast, coyotes are now found from Nova Scotia to Florida and exist at high enough population densities in virtually every region to have become an important component of the ecological community. Therefore a solid understanding of coyote ecology is necessary for conservation planning at many levels. This paper summarizes what is known of the ecology of coyotes in northeastern North America (including New England, New York and Canada east of the Ontario-Québec border), and identifies areas of research requiring immediate attention. While much is known regarding coyote natural history and ecology in this region, there are also major gaps in our knowledge base. In particular, four aspects of coyote ecology are suggested as priorities for future research:



The demographics and growth rates of the northeastern coyote populations.

The role of northeastern coyotes in structuring communities.

The important parasites and diseases of northeastern coyotes.

The impact of wolf-coyote hybridization on the population genetics and ecology of northeastern coyotes.

A focus on these research areas will allow for informed management decisions in the face of an array of conservation priorities in the Northeast.



INTRODUCTION:

The History and Causes of Coyote Range Expansion

Large carnivores disappeared from most of the eastern United States by the early 20th century. While many predators are now reestablishing and increasing in numbers as a result of decreased predator control efforts and increased conservation efforts, wolves (*Canis lupus*) and puma (*Felis concolor*) have not returned in large numbers to most of their former range. In their place the coyote (*Canis latrans*) has become widespread, occupying virtually every habitat in eastern North America. Coyote ecology in the eastern United States is poorly understood, but it is assumed that as coyote populations increase, the potential for top-down direct and indirect impacts on a broad array of organisms and habitats also increases. For better or worse, interactions with humans will also increase, resulting in greater public scrutiny of land management practices and an increased call for information on coyote populations. A better understanding of the ecology of current coyote populations is essential to predict coyote dynamics in the future and to predict the consequences of increasing coyote populations on other taxa and habitats.

Although the coyote is common in the Midwest, it was virtually unknown to European settlers of eastern North America. Lewis and Clark described it as a “prairie wolf” when in 1804 they caught their first glimpse of the species on the eastern edge of present day Nebraska (Ambrose 1996). Over the past 200 years, however, the coyote has steadily expanded its geographical range (Moore and Parker 1992). Coyotes were reported in Michigan about 1900 and in southern Ontario by 1919 (Ontario Dept. of Lands and Forest 1972). Between the 1920’s and 1940’s occasional reports of coyotes were made in East Coast states, but nowhere was the species common. In the Northeast, coyotes were

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America**

first reported in New York in 1925 (Bromley 1956), southwestern Québec, Maine, New Hampshire and Vermont in the 1930s - 1940s (Rand 1945, Pringle 1960, Richens and Hugie 1974), southeastern Québec in the early 1970s (Georges 1975), Nova Scotia in 1977 (Moore and Millar 1984), and Newfoundland in the early 1990s (Parker 1995), although in some cases the actual colonization may have preceded these dates.

Since these early colonization reports, the range and density of coyotes has dramatically expanded. The colonization rate in Maine between 1968 and 1974 was estimated at 1867 km²/yr (Richens and Hugie 1974), and by 1987, 1500 individuals were killed in Maine (Harrison 1986). The 1992-1993 Nova Scotia trapping season resulted in a harvest of 1276 coyotes (Patterson 1995). In Pennsylvania the harvest by hunters in the early 1990's exceeded 6000 (Pennsylvania Game Commission 1998). Today the species is found throughout virtually all of eastern North America (Whitaker and Hamilton 1998), including several seemingly isolated geographical regions such as Cape Cod and the Elizabeth Islands of Massachusetts, Mount Desert Island, Maine, Cape Breton and Prince Edward Islands, Nova Scotia, and Newfoundland (O'Connell et al 1992, Parker 1995) as well as urban habitats such as Central Park and Van Cortland Park in New York City (Bryant 1997, Martin 1999).

What has allowed this dramatic range expansion? Three hypotheses exist. First, the eradication of the gray wolf from throughout its former range may have reduced the competitive pressures limiting coyotes to midwestern and western North America. Coyotes and wolves are interference competitors; that is, wolves limit coyote access to resources by direct aggression. Field studies in regions where wolves and coyotes overlap indicate that coyotes are excluded from wolf territories and that wolves will go out of their way to kill coyotes (Fuller and Keith 1981, Berg and Chesness 1978, Litvaitis 1992, Peterson 1996, Crabtree and Sheldon 1999, Carbyn 1982, Johnson et al. 1996, Paquet 1991, Thurber et al. 1992). In regions such as the Greater Yellowstone Ecosystem and Isle Royale, Michigan where wolves have recently recolonized or been reintroduced and the wolf population has rapidly grown, coyote densities have declined dramatically and coyote microhabitat use has changed to avoid wolves (Krefting 1969, Crabtree and Sheldon 1999, Finkel 1999). These findings suggest competitive release of coyotes following wolf declines, and this may have occurred in the Northeast.

Second, the casual and perhaps common translocation of coyotes by humans may have hastened the range expansion or may even be the chief cause of coyote colonization of particular regions. This may have been more important in the southeastern United States where at least 18 releases occurred (Parker 1995, Hill et al. 1987, Bourne 1991). Whitaker and Hamilton (1998) suggest that in some cases in the southeast, fox hunters released coyotes that were mistakenly shipped to them because of their resemblance to fox pups. Releases or escapees also occurred in Maine, New York, New Jersey, and Pennsylvania (Parker 1995). Yet as Parker's evidence clearly shows, these accidental or intentional translocations of a few individuals would have little long-term impact on the overall genetic structure or population dynamics of coyotes in the Northeast. Coyotes were steadily expanding their geographic range, independent of direct assistance by humans.

Third, the altered habitat and community structure caused by increasing human population density may have opened additional habitat to coyotes. The eastward expansion of coyotes coincided with the conversion of habitat in the region by intensive logging and agricultural development (Larivière and Crête 1992, Parker 1995). This habitat conversion also favored white-tailed deer in Atlantic Canada, and both species expanded their range northwards to the limits imposed by snow cover and resource availability (Parker 1995).

While all three mechanisms may help explain the success of coyotes in the Northeast, some attention should be placed on understanding the relative likelihood or explanatory power of each hypothesis. This is important for several reasons. First, recolonization of the Northeast by wolves – naturally or by means of reintroduction is becoming an increasingly real possibility (Mladenoff and Sickley 1998, Harrison and Chapin 1997, 1998, Wydeven et al. 1998, Paquet et al. 1999). If coyotes have been successful in some regions primarily due to the absence of competition from wolves, then it is possible that wolf reintroduction or natural recolonization might be slowed by the presence of coyotes, might lead to localized declines in coyote densities in regions where they are currently numerous, and might result in altered foraging ecology of coyotes sympatric with wolves. The broader implications of this are unclear. In northwestern Montana the recolonization of wolves resulted in altered coyote diets, and possibly as a result of the latter, coyote body size and group size increased (Arjo 1998).

Second, fossil evidence from Maryland, Pennsylvania, and New Brunswick suggests the presence of coyotes in the Northeast during the Pleistocene (Gipson 1978, Stewart 1976, Nowak 1978). Nonetheless, if recent coyote range expansion in the Northeast was aided extensively by the release of animals, then the perception of the coyote as a natural immigrant to the East Coast could be supplanted in the minds of some people by the concept of the coyote as non-native alien species. This could, potentially, have environmental policy implications. It should be emphasized however, that the evidence does not support intentional and unintentional releases as a significant factor in influencing the current distribution of coyotes in the Northeast (Parker 1995).

Third, the eastern half of North America is not in a state of landscape stasis. Rather, it is subject to continuing change due to anthropogenic factors ranging from urban sprawl to global climate change. For instance, in the Northeast the conversion of abandoned farmland to second-growth woodlands, and the reduced presence of large-scale forestry is resulting in increased and aging forest cover and a less agricultural landscape (Cronon 1983, Foster 1993, Fuller et al. 1998, Ray 2000). Again, the implication of this altered landscape for the future of coyotes and their importance in local communities in the Northeast is unclear. Recent evidence generated from a long-term wolf study indicates that predator behavioral response to global climatic variation can dramatically alter ecosystem function at lower trophic levels (Post et al. 1999). Coyotes can similarly influence lower trophic levels, but predicting the outcome of this influence will be difficult in the Northeast because the effects of habitat succession and climate change must be simultaneously considered.

The eastward expansion of coyotes coincided with the conversion of habitat in the region by intensive logging and agricultural development

The Need for Greater Insight on the Ecology of Northeastern Coyotes

As a top-predator, the potential for direct and indirect influences on a broad array of organisms and habitats are great

What are the impacts of coyotes naturally colonizing northeastern North America? One way to address this question is to examine the breadth of questions being examined by researchers in the Midwest and West (Table 1). As a large top-predator, the potential for top-down direct and indirect impacts on a broad array of organisms and habitats are great. For instance, predator-prey interactions involving coyotes and ungulates have received extensive attention (see below), and in some regions coyotes may limit, and perhaps even regulate prey populations. Several unique ungulate populations, already reduced to small numbers for reasons unrelated to coyotes, are currently threatened with extinction due to predation by coyotes (e.g. Crête and Desrosiers 1995). Similarly, the presence or absence of coyotes in habitat fragments in southern California has recently been associated with mesopredator release and dramatically altered rodent and bird communities (Crooks and Soulé 1999). Foxes are competitors with coyotes (Gese et al. 1996a; Johnson et al. 1996), and in many regions coyotes are principal sources of fox mortality (Ralls and White 1995; Cypher and Spencer 1998) or alter fox spatial dynamics (Sargeant et al. 1987; Theberge and Wedeles 1989; Harrison et al. 1989; Major and Sherburne 1987). If the increase in coyotes influences the population dynamics of foxes and other mesocarnivores, a cascade of ecosystem effects may occur, including alteration of rodent and rabbit communities, and changing pressures on plant communities (Wagner & Stoddart 1972; Knowlton et al. 1977; Vander Wall 1990; Longland 1995, Henke and Bryant 1999). Thus, the direct influence of coyotes on small mammals may indirectly influence plant community structure. In addition, because coyotes are generalist predators, they can attain high densities relative to more specialized carnivores and as a result, outcompete them. For instance, competition for resources occurs between coyotes, lynx (*Felis lynx*) and bobcat (*F. rufus*); increased coyote densities may result in declines in these felids (Schmidt 1986, Litvaitis and Harrison 1989, Fox 1990). Thus a better understanding of the ecology of current coyote populations is essential to predict coyote dynamics in the future and to predict the consequences of increasing coyote populations on other taxa and habitats.

In addition, increased coyote numbers will result in increased interactions between a large predator and the public. This interaction may be perceived as negative on two fronts. First, the killing of domestic animals, livestock, and the perceived threat to humans suggests safety concerns and risk of economic loss. Second, coyotes and human hunters sometimes seek the same prey, suggesting possible competition for resources.

Coyotes will kill domestic animals and livestock such as cats, dogs, chickens, sheep, and cattle, and much of the research on coyotes in western North America is oriented directly or tangentially towards addressing this issue. Because of the reputation of coyotes as predators of livestock, it is important to examine the impact of this behavior. In 16 western U.S. states, livestock deaths due to coyotes result in estimates of annual economic losses of between \$4.4 and \$27 million, and more than 97,000 coyotes per year are killed at an annual cost approaching \$20 million (Gee et al. 1977; O'Toole

1994). Coyotes are responsible on average for 87% (range: 46-100%) of known domestic sheep losses to predators (Table 2). Using Nevada as an example, in 1992 a total of 3,178 events were reported in the state, and 7.5% of Nevada's domestic sheep lambs were killed by coyotes (O'Toole 1994). Predation on cattle is also a serious problem. Approximately 0.6% of the calves (based on 540,000 adults grazing on Nevada's public lands) were lost to coyotes. Claimed losses in the state amounted to about \$240,000, and included 356 adult and 1,312 young sheep and 25 adult and 49 young cattle (National Agricultural Statistics 1992). In addition, more than 6,000 coyotes were removed (O'Toole 1994). Many additional losses and removals may go unreported. Clearly, the real and perceived losses due to predators are economically significant in these western regions, raising genuine concerns about the protection and economics of livestock and farm animal production in the Northeast.

Table 1.

Issue	Sites	Key recent references
1. Coyotes as keystone predators	California, Texas	Crooks and Soulé 1999, Henke and Bryant 1999
2. Competition between canid species	Wyoming, California, Alaska	Johnson et al. 1996; Cypher and Spencer 1998; Thurber et al. 1992
3. Coyote behavioral ecology	Wyoming	Gese 1998
4. Coyote population dynamics	New Mexico, Wyoming	Windberg 1995, Windberg et al. 1997
5. Coyote disease ecology	Texas, Wyoming	Clark et al. 1994, Gese et al. 1997, Pence and Windberg 1994, Pence 1995
6. Coyote foraging ecology and predator-prey relationships	Colorado, Wyoming	Bartmann et al. 1992, Gese et al 1996b
7. Coyote depredation on livestock	California, Utah	Sacks et al. 1999a,b; Wagner and Conover 1999; Shivik et al 1996; Knowlton et al. 1999

Examples of ecological issues recently examined by coyote researchers throughout North America.

While attacks on humans have occurred in the Northeast, these events are relatively rare

Table 2.

Sampling of estimated sheep losses to coyotes based on field surveys.

Column A = % of population lost to coyotes.

Column B = % of all predator losses due to coyotes.

Location	Total sheep	A	B
1) Nevada	2466	5	46
2) Montana	2041	21	97
3) New Mexico ^a	994	4	77
4) New Mexico ^a	997	5	100
5) Montana	3712	16	99
6) Idaho ^b	16669	1	93
7) Utah	16000 (ca.)	4	93
8) Wyoming	3427	6	78
9) California	1562	8	99

^awith limited predator control.

^bmean value for three years.

References:

- 1 Klebenow & McAdoo (1976)
- 2 Henne (1975)
- 3-4 Delorenzo & Howard (1976)
- 5 Munoz (1976)
- 6 Nass (1977)
- 7 Taylor (1977)
- 8 Tigner & Larson (1977)
- 9 McAdoo & Klebenow (1978)

How issues of livestock loss, which many perceive as unique to western North America, will play out in the Northeast remains to be seen. Nonetheless, at extreme levels, predation on domestic animals by coyotes may result in pressure from the public to increase predator control programs (Kellert 1985). This interaction may also intensify fears of coyotes attacking humans and their pets. While attacks on humans are relatively rare in the western U.S., they do occasionally occur (Howell 1982, Carbyn 1989), and 3% of U.S. National Park Service units reported coyotes displaying aggressive behavior towards humans. This aggressiveness was often associated with humans feeding coyotes (Bounds and Shaw, 1994). Reports of coyotes killing pets have now become rather commonplace in the Northeast (e.g. Bider and Weil 1984, Smith 1992, Parker 1995). Attacks on humans have also been reported. In 1988 a young girl was attacked in Cape Breton Highlands National Park, in 1991 an adult male was attacked on West Mountain, Vermont, and in 1998 a young boy was attacked in Cape Cod, Massachusetts (Smith 1992, Parker 1995, Ray 2000, Myers 1998).

Coyotes and human recreational hunters compete for prey such as deer, and this competition has resulted in calls for predator control and expanded hunting seasons on coyotes (e.g. Hilton 1992). In other words, direct and indirect

interactions between coyotes and the public will undoubtedly result in increased public scrutiny of land management practices and increased calls for information on coyote populations. Increased pressures to extend hunting seasons for coyotes or to enact predator control programs are worthy of skeptical concern because coyotes may be strongly density-dependent breeders. Therefore, without large and sustained efforts to control coyotes beyond the bounds of some local area of interest, regional control efforts are likely to be unsuccessful in the long run, and perhaps even stimulate growth in the coyote population (Knowlton 1972, Connolly and Longhurst 1975, Connolly 1978, Sterling et al. 1983, Stephenson and Kennedy 1993, Davison 1981).

Finally, recent attention has been given to the possibility of the return of wolves to the Northeast (Mladenoff and Sickley 1998). Since wolves and coyotes are direct competitors for resources, share many of the same diseases, and may hybridize in some regions, attention should also be given to the ecological role of coyotes in the region and the interactions that coyotes and wolves are likely to have should such a reintroduction or natural recolonization occur.

The breadth of these issues indicates the need to understand the ecology and demographics of coyotes in northeastern North America. Therefore the remainder of this paper focuses on the important ecological issues surrounding the coyote in northeastern North America by summarizing what is already known and identifying aspects of the ecology of coyotes in the Northeast that remain unresolved. These issues include aspects of the evolutionary, behavioral, population, and community ecology of coyotes.



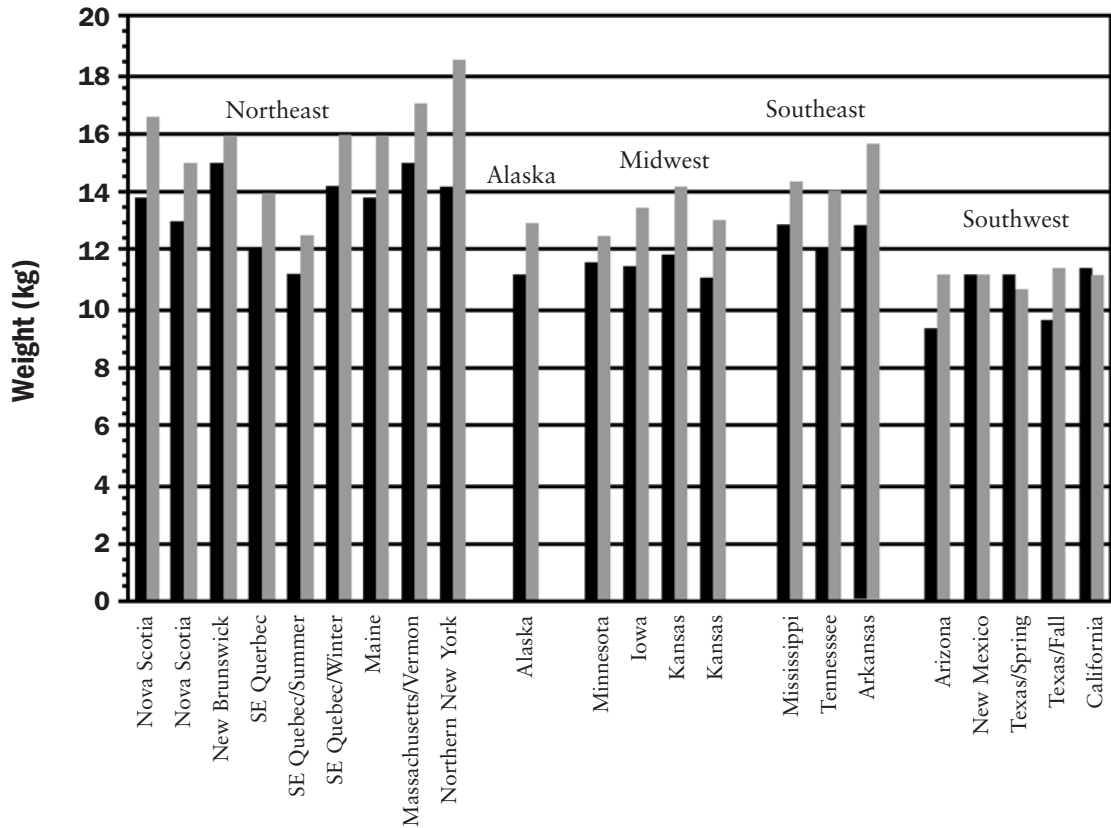


THE ECOLOGY OF NORTHEAST COYOTES:

Morphology and Ecological Genetics of Northeastern Coyotes

Much has been made of the fact that coyotes in the Northeast may be larger than their counterparts in other parts of their geographic range. The evidence for this larger size is not, however, unambiguous. As Parker (1995) notes, “Although larger than its western cousin, [...the coyote of Atlantic Canada...] is only slightly heavier than coyotes in Kansas and Minnesota and no larger than coyotes in New England. In fact, coyotes in the southeastern states are as large, if not larger than coyotes in the northeast (p. 36)”. Similar sentiment was expressed by Hilton (1978), who also noted that the size of coyotes is often overestimated in the field, and that erroneous reports of very large (27 – 36 kg) coyotes are “not uncommon”. Figure 1 shows the range of average values of body mass that have been published for coyotes from the Northeast and elsewhere. Although Northeast coyotes were larger than coyotes from the Midwest and Southwest, they were not significantly larger than those from the Southeast. While valid reports of particularly large specimens (in the 23 to 30 kg range) exist (Parker 1995), these are rare and no single region stands out as being outside the range of normal average body mass. The image of coyotes as being particularly large may in part be due to the inclusion of coydogs (coyote-domestic dog hybrids) which may occasionally reach the 27-32 kg range (Parker 1995). On the other hand, there is evidence that coyotes in the Northeast as a whole may be somewhat, although not extremely, greater in size than coyotes from elsewhere in their range (Thurber and Peterson 1991, Fig. 1). It should

Figure 1. Mean adult weight (kg) of female (solid black) and male (shaded gray) coyotes, subdivided by locality.



References: Nova Scotia - Parker 1995, Sabeau 1993; New Brunswick - Moore and Millar 1986; southeastern Quebec - Huot et al. 1995, Poulle et al. 1995; Maine - Richens and Hugie 1974; Massachusetts and Vermont - Lorenz 1978; northern New York - Kendrot 1998; Alaska - Thurber and Peterson 1991; Minnesota - Berg and Chesness 1978; Iowa - Andrews and Boggess 1978; Kansas - Gier 1968, Boggess and Henderson 1977; Mississippi - Edwards 1996; Tennessee - Stephenson and Kennedy 1993; Arkansas - Gipson 1978; Arizona - Fisher 1980; New Mexico - Young and Jackson 1951; Texas - Windberg et al. 1991; California - Hawthorne 1971.

Statistical analyses: Data were analyzed separately for males and females by Analysis of Variance (ANOVA) and post-hoc Bonferroni tests. Mean values were used for states and provinces with > 1 value or with separate seasonal values (Quebec, Kansas, Texas, Nova Scotia). Alaska was excluded from analyses because only one data point was available. ANOVAs revealed significant differences ($p < 0.001$) among regions for both males and females. For females, post-hoc analyses revealed significant differences ($p < 0.05$) between the northeast and midwest, northeast and southwest, midwest and southwest, and southeast and southwest. No differences were found between northeast and southeast females ($p = 0.087$), and midwest and southwest females ($p = 0.477$). For males, post-hoc analyses identified differences ($p < 0.05$) between the northeast and midwest, northeast and southwest, and southeast and southwest. No differences were found between northeast and southeast males ($p = 0.308$), midwest and southwest males ($p = 0.119$), and midwest and southwest males ($p = 0.585$).

also be noted that body mass may vary considerably throughout the year. Poulle et al. (1995) found that coyotes collected in southeastern Québec were 27-28% heavier during the autumn-winter than during summer. Habitat differences can also influence body mass. Tremblay et al. (1998) reported that during the late summer, coyotes inhabiting rural landscapes were heavier than coyotes inhabiting neighboring forested regions in southeastern Québec.

Two non-exclusive explanations may underlie the possible larger body size of northeastern coyotes. First, the larger body size may be a response to prey size and availability. Thurber and Peterson (1991) found a significant relationship between coyote body size and longitude (but not latitude). They attributed this relationship to the large size of coyotes from New Hampshire, and suggested that a phenotypic response to food supply may account for most variation in body size of coyotes. In support of this, Arjo (1998) found that body size of coyotes in northwestern Montana increased after wolf reintroduction due to greater use of ungulates killed by wolves. In contrast, Larivière and Crête (1993), attributed the possibly larger body size of northeastern coyotes to a genetic adaptation to the use of larger prey – in particular, white-tailed deer (*Odocoileus virginianus*), or perhaps to hybridization with wolves (see below). Both pairs of authors agreed that these hypotheses could not be completely assessed without additional genetic analyses.

Second, the large body size of northeastern coyotes may be attributable to hybridization with wolves and/or domestic dogs in the recent past (Hilton 1978, Lawrence and Bossert 1975, Mengel 1971, Nowak 1978, 1979, Silver and Silver 1969, Voigt and Berg 1987, Wilson et al. 1999). Thurber and Peterson (1991) have argued against the importance of hybridization as an explanation for the large body size of northeastern coyotes. They note the relatively small size of Alaskan coyotes (which colonized the Kenai Peninsula in the early 1900's), which they suggest might face the same hybridization pressures (see below) as coyotes in northeastern North America. In agreement with this argument is the small body size of Minnesota coyotes, where a wolf-coyote hybrid zone exists, compared to coyotes in the Northeast (Fig. 1).

Hybridization between wolves and coyotes is possible in the wild, and a hybrid zone exists in northeastern Minnesota, southern Ontario, and southern Québec (Lehman et al. 1991, Wayne and Koepfli 1996). Mitochondrial DNA (mtDNA) analyses of this hybrid zone suggest that this phenomenon is associated with the inability of male wolves to find conspecific mates. Coyote mtDNA genotypes occurred in wolves, but not vice versa, indicating that most hybridization took place between male wolves and female coyotes whose offspring then backcrossed with wolves. As Wayne and Koepfli (1996) noted, this sort of asymmetric hybridization is consistent with the expectation that larger male wolves can dominate smaller female coyotes, but that the opposite is not true. That is, smaller male coyotes are unable to mate with larger female wolves. Nuclear DNA analyses (Roy et al. 1994, Wilson et al. 1996) corroborate the mtDNA analyses, and suggest that as few as two or three hybridization events per generation could cause the allele frequencies observed among coyotes and wolves in the hybrid zone.

Whether coyotes in northeastern North America and outside of the known coyote-wolf hybrid zone have been significantly influenced genotypically by

Larger body size in the Northeast may be a response to prey size and availability, or to hybridization with wolves

**The biological
significance of
the genetic
makeup of
northeastern
coyotes remains
unclear**

hybridization with wolves has not been decisively answered. Lawrence and Bossert (1975) used discriminant analyses of skull measurements to conclude that skull ratios of coyotes from New Hampshire, Vermont and Massachusetts were intermediate between wolves and more western coyotes. More recently, Wayne and Lehman (1992) used mtDNA markers to assess the genetic origins of eastern coyotes. They found that coyotes in the New England states (n = 16 from Maine and n = 1 from Connecticut) have mtDNA genotypes that are also shared by coyotes from Michigan, Minnesota, and Québec, and wolves from southeastern Ontario and Québec. These mtDNA genotypes may reflect coyote genotypes that have introgressed into the wolf population, rather than vice versa. None of the coyotes sampled were found to have wolf genotypes. Nonetheless, the authors concluded that the eastern coyote phenotype probably reflects a mixed genetic heritage. It should be noted, however, that because the analyses did not examine coyotes from throughout the Northeast (for example, New York) and because the analyses were limited to mtDNA (which is strictly maternally inherited and thus cannot be lost from a maternal lineage), it is difficult to assess the relative frequency of such hybridization events. Nonetheless, gene flow from wolves to coyotes may have occurred as a result of backcrossing by first generation hybrids into the larger coyote population (Wayne and Lehman 1992). Wilson et al. (1999) recently examined the mtDNA of a wolf killed in 1893 in New York and identified a “coyote-related” genotype, which the authors suggest may in fact be derived from hybridization with eastern Canada wolves (referred to by Wilson et al. as *C. lycaon*), which in turn may be more closely related to coyotes than gray wolves. In addition, an analysis of nuclear microsatellite DNA also suggests that northeastern coyotes may in fact represent a hybrid between eastern Canadian wolves and coyotes. The biological significance of Wilson et al.’s (1996, 1999) findings are still unclear, and consensus by the research community on the genetic makeup of northeastern coyotes has yet to be reached.

Hybridization between coyotes and domestic dogs is possible in captivity and in the wild (Mengel 1971, Mahan et al. 1978), and its occurrence has been documented in the Northeast (Nowak 1978). However, the ecological importance of this type of hybridization appears minor. Morphological characteristics of domestic dogs are rarely found in wild coyotes, and genetic analyses have not identified domestic dog alleles within northeastern coyote populations (Wayne and Lehman 1992, Nowak 1978). In addition, reproductive studies indicate that coyotes and domestic dogs have difficulty successfully crossbreeding in the wild due to a phase shift in reproductive cycles of first generation offspring (Mengel 1971, Kennelly 1978).

The complex genetic origin of the northeastern coyote and the potential for hybridization with wolves living at low densities suggests the need for considerable attention to the possibility of future hybridization should wolves return or be reintroduced into the Northeast (Paquet et al. 1999). Unless sufficiently large numbers of wolves are reintroduced within a relatively short period of time, wolves may be unable to find suitable conspecific mates and will therefore mate with coyotes. Coyote-wolf hybridization does not appear to be a problem in Yellowstone National Park, perhaps because sufficient numbers of wolves were simultaneously introduced.

Northeastern Coyote Behavioral Ecology

Coyotes have a rich social structure that has attracted considerable interest. The social organization is variable, ranging from solitary transient individuals, to solitary territorial individuals, to packs. The social organization is also responsive to environmental constraints. In general, however, packs are made up of a pair of mated adults and their offspring. Packs may also contain non-breeding adults who assist in the care of offspring.

An understanding of coyote pack size and structure is important for predicting predator-prey interactions and population densities. Traveling and foraging group size increases during the winter, although the absolute pack size is largest during the late spring and early summer following the birth of new pups. During winter, groups of 1, 2, and 3-5 were observed on 37%, 28% and 35% of occasions, respectively, in Québec (Messier and Barrette 1982). In Nova Scotia groups were typically 3-4 (Patterson 1995). In Maine coyotes usually travel singly or in pairs (Major and Sherburne 1987). In the central Adirondacks, pack members traveled and hunted together during the winter and alone during the summer (Brundige 1993). In some regions, high densities may favor larger group sizes due to delayed dispersal, which in turn may provide opportunities to exploit larger prey (Bekoff and Wells 1980, Bowen 1981, Messier and Barrette 1982, Patterson 1995). The importance of this has not been well explored in the Northeast. Packs are also sensitive to membership disturbance; Brundige (1993) noted the breakup of a pack and dispersal of subordinate animals after the death of a dominant female.

Coyotes in eastern Maine were crepuscular; most active in the early morning (0400-0800) and in the late afternoon and evening hours (1600-2400). While not completely inactive during other periods, they often rested for up to four hours during these periods. This activity pattern was consistent across seasons (Caturano 1983). However this is not always the case. In western Maine, Major (1983) found activity to be variable with no distinct patterns. This was also reported by Brundige (1993) in the Adirondacks, who also reported that coyotes traveled an average distance of 24.4 km per day. In Nova Scotia, coyotes were most active in the evening, and traveled 10.7 km per day (Patterson 1995). The activity patterns of coyotes can be influenced by human disturbances, especially exploitation. For instance, in Colorado coyotes have been observed to increase diurnal movements following cessation of persecution by humans (Kitchen et al. 2000).

Coyotes communicate through auditory, olfactory and visual means. While poorly studied in the Northeast, a few observations on these communication patterns have been made. Howling and urine scent-marking play important roles in territory maintenance and in communicating within family groups (Barrette and Messier 1980, Lehner 1978, Patterson 1995). In Nova Scotia, adult and juvenile pack members yip-howled almost nightly from late May through autumn, with the exception of windy overcast nights when howling was not observed (Patterson 1995).



Coyotes have a rich social structure ranging from solitary transients, to solitary territorial individuals, to packs

Coyote Foraging Ecology in the Northeast

The coyote is an opportunistic and generalist feeder. Analyses of diets throughout the range of the species have identified food items as varied as large and small vertebrates, invertebrates, and fruit. Live prey and carrion are both utilized. There can be significant seasonal changes in diet in response to changes in food availability. Thus comparisons of coyote diets should be made with an understanding of the habitat type and the period of study. Nonetheless, the diets of coyotes have been subject to study in many parts of the Northeast, and a general pattern has emerged: white-tailed deer and snowshoe hare (*Lepus americanus*) are important year-round, and fruit is important in the late summer and fall.

The most important prey of northeastern coyotes are white-tailed deer and snowshoe hare

For instance, several dietary studies have been performed in Maine. Dibello et al. (1990) reported that snowshoe hares and deer were the most important animal components of the diet, but 23-55% of the diet was made up of fruits such as blueberries (*Vaccinium angustifolium*), raspberries (*Rubus* spp.), and pincherries (*Prunus pennsylvanica*). Hares were used throughout the year, but deer were used primarily during the winter. During more severe winters, the use of deer increased and hares decreased. Dibello et al. (1990) were, however, unable to determine whether a coyote had actually killed the deer. Litvaitis and Harrison (1989) and Major and Sherburne (1987) report similar results. In the winter and spring, deer and snowshoe hare dominated the diet, whereas in the summer and fall blueberries dominated, followed in importance by snowshoe hares, small mammals, deer, and birds. Also in Maine, independence of pups was accompanied by a shift in diet from parental-supplied white-tailed deer to blueberries (Harrison and Harrison 1984).

The importance of deer, snowshoe hare, and fruit is also seen in New York (Brundige 1993), Québec (Samson and Crête 1997, Messier et al. 1986), New Brunswick (Parker 1986, Moore and Miller 1986, Morton 1988), and Nova Scotia (Patterson 1995). Where one of the preferred foods occurs at lower densities, coyotes may focus on another species, such as raccoons (*Procyon lotor*) on Mount Desert Island in eastern Maine where snowshoe hares are rare (O'Connell et al. 1992) and porcupine (*Erethizon dorsatum*) in Forillon National Park, Quebec where white-tailed deer are rare (Fortin 1995).

An important conservation and wildlife management issue involving coyotes in the Northeast is their impact on native ungulates: caribou (*Rangifer tarandus*), moose (*Alces alces*), and white-tailed deer. Remains of moose have been found in the scats of coyotes (Litvaitis and Harrison 1989), but these are rare occurrences (5 in 1149 coyote feces) and it is unclear if they are due to scavenging or predation on neonates. In Maine and Gaspésie National Park in southeastern Québec the remains of moose in scats are likely from scavenging (Hilton 1978, Samson and Crête 1997).

Coyotes can significantly impact caribou populations, especially if the population is small or isolated. For instance, the colonization of Gaspésie National Park by coyotes resulted in a decline in the park's caribou herd (Crête and Desrosiers 1995). In this case the relatively few calves killed by coyotes were sufficient to cause a decline in the caribou population. A predator control program was put in place for three years to allow the survival rates of caribou calves to rebound.

Coyotes have been shown to kill white-tailed deer throughout the Northeast. In the Adirondacks of New York, coyote diets are now dominated by white-tailed deer (Brundige 1993). Fawns represent almost a third of deer consumed in June. In southwestern Massachusetts, the cause-specific mortality rate of deer fawns associated with predation by coyotes was 5.8% (Decker et al. 1992). While much of the deer consumed may be fawns or carrion, coyote predation on adults may be significant when deep snow impairs deer movements (Messier and Barrette 1985). In New Brunswick, where deer reach the northern edge of their range, annual adult survival of deer appears dependent on either hunter harvest or coyote predation (Whitlaw et al. 1998). In Kejimikujik National Park, Nova Scotia, the white-tailed deer population declined considerably following coyote colonization of the region. In Kejimikujik, snow depth appeared to be a contributing factor for most of the winter deer kills (Patterson 1995).

Coyote group size influences the relative importance of prey species. Pairs of coyotes relied more on deer than did solitary individuals, and packs of 3 or more coyotes relied more on deer than did pairs (Messier et al. 1986). In Québec, group-living, territorial coyotes were responsible for most predation on adult deer (Messier and Barrette 1985). Similarly, in Nova Scotia groups of coyotes were more successful at killing deer than were solitary coyotes (Patterson 1995)

The underlying questions faced by wildlife managers and conservationists regarding the impact of coyotes on deer are two-fold. First, do coyotes kill prey that would otherwise die for reasons such as limited food availability or severe weather (compensatory mortality), or is mortality from coyotes additional to these other sources of mortality (additive mortality)? In other words, does the arrival of coyotes signify a new burden for ungulate populations, or does the mortality caused by coyotes simply substitute for some other cause of mortality and have no broad effect on ungulate numbers or population dynamics. In Colorado, for instance, Bartmann et al. (1992) experimentally demonstrated that a three year coyote removal program had no impact on mule deer fawn survival, as the decline in predation on fawns was offset by an increase in fawn starvation. Thus because there was no net increase in fawn survival, predation by coyotes on fawns was judged compensatory rather than additive. Similar studies are required in the Northeast before coyotes can be judged to have significant impacts on ungulate populations. In New Brunswick, where deer reach the northern edge of their range, adult survival appears dependent primarily on hunting in those populations that are exploited, and otherwise on predation by coyotes. In this case, predation may be additive where the deer population is also exploited (Whitlaw et al. 1998).

Second, if coyote-caused mortality is additive, is the ungulate population of interest regulated by coyotes (implying density dependent predation), or are predation levels maintained over a range of prey densities (density independent predation)? The former scenario would imply a change in prey numbers to a new equilibrium. The latter situation, however, means that coyotes may be responsible for prey declines, and that when a prey population is decreased due to disease, harsh winters, or overhunting, predation by coyotes could have a strong influence of prey population growth rates. This influence could perhaps even cause predator-pits; regions where predators limit the ability of a prey species to rebound from some perturbation (Parker 1995).

An important conservation and wildlife management issue involving coyotes in the Northeast is their impact on native ungulates

It cannot be assumed that coyotes always take the weakest deer

It cannot be assumed that coyotes always take the weakest deer. Several studies in the Northeast have found that coyotes killed deer that were in better condition than those in the general deer population (Brundige 1993, Major and Sherburne 1987, Lavigne 1992, Messier et al. 1986). Lavigne (1992) noted that if one assumes that good condition in winter equates with surviving to reproduce the following spring, and thereby an increasing population density of deer, than predation on deer by coyotes is additive to other sources of mortality such as hunting and road-kills. Unclear, however, is the impact of hunting by humans on coyote use of adult deer. Several dietary studies have attributed the high occurrence of deer in the winter diet, at least in part, to feeding on injured or dead deer not found by human hunters (Hamilton 1974, Edwards 1996, Lee and Kennedy 1986, Ozaga and Harger 1966, Toweill and Anthony 1988, Berg and Chesness 1978, Wooding 1984).

In the New York Adirondacks, coyote diets have been studied since the 1950's. Between 1956 and 1961 snowshoe hares were of primary importance year-round, with deer being equally as important in the winter but less so in the summer. In the summer and fall fruit was second in importance (Hamilton 1974). The use of deer was higher in the late 1970's (1975-1980) than in the late 1950's despite a lower deer population during the 1970's. Snowshoe hare also remained important (Chambers 1987). Still more recently, Brundige (1993) studied coyote food habits from 1986-1989 and found that deer remained the most important component of the diet, especially during the winter and spring. Nonetheless, deer comprised a smaller portion of the diet than in the 1970's. Brundige suggests that coyotes had little impact on the deer population in the 1950's when deer densities were high and coyote densities were low. In the 1970's, however, coyote predation was high and deer numbers low. During this period, coyotes may have depressed deer population levels. In the 1980's predation by coyotes apparently had limited impact on deer abundance (Brundrige 1993).

In agricultural regions the diets of coyotes can differ dramatically from that observed in more undisturbed sites. In Vermont, Person and Hirth (1991) frequently observed coyotes feeding on cattle carcasses dumped by farmers. Bergeron and Demers (1983) examined the stomach contents of 84 coyotes killed by trappers and government predator control agents in southern Québec. Domestic animal carrion (cows and pigs) occurred in 30% of the animals, and were the most important component of their diet, followed in order by snowshoe hares, small mammals, deer, woodchucks (*Marmota monax*), and raccoons. Tremblay et al. (1998) found that in southeastern Québec forest coyotes consumed more fruits during the "pup initiation" stage (mid July to late September) than did rural coyotes that relied more on small mammals.

Demographics of the Northeastern Coyote

Coyotes are seasonally breeding, monestrous canids. Females are able to commence breeding as yearlings, although pregnancy rates are typically lower for yearling females than for older age classes. Yearling males may be unable to breed because of a lack of sperm and an inability to produce enough serum testosterone to sustain copulatory behavior (Amoss and Hodges 1995, Kennelly 1978). In the Northeast, mating generally occurs in late January - mid

February (Hilton 1978, Parker 1995, Harrison and Gilbert 1985, Chamber 1992). Regression of the adult testis begins in March and by June sperm production has ended (Kennelly 1978). Gestation ranges from 60-63 days (Kennelly 1978), and birth usually occurs mid-late April (Harrison et al. 1991, Caturano 1983, Hilton 1978), emergence from dens occurs in late May at age 4-5 weeks, and abandonment of the den by the young occurs at about 8-10 weeks (Harrison et al. 1991).

Characteristics such as percentage of females breeding, litter size, and sex ratios can vary considerably between populations as well as between years within a population. There have been few studies describing these parameters for northeastern coyote populations. Poulle et al. (1995) report that based on examination of uteri of coyotes collected in southeastern Québec, 29% of 3-5 yr olds (n=24) and 75% of females > 5 yrs (n = 8) had placental scars indicating they were reproductive. In a three year study (1977-1979) in southeastern Québec, Jean and Bergeron (1984) found that ovulation rates of females < 1 year old were lower than subadults (1-2 years old) and adults (> 2 years old), although there was no significant difference between subadults and adults. Litter sizes, averaging 7.1 across all age classes, also were greater in older individuals (Fig. 2). In other northeastern regions, mean litter sizes ranged from 6.4 to 7.0 (Lorenz 1978, Hilton 1976, Chambers 1992). These litter sizes are generally larger than those found outside of the Northeast and it is possible that values may decline as populations expand and population densities increase in the Northeast (Jean and Bergeron 1984, Chambers 1992).

Sex ratios of coyotes vary considerably as a consequence of resource abundance, population expansion, and the intensity of predator exploitation. Sex ratios that favor females are usually in areas of intense control (Knowlton 1972). Excluding the possibility of sex-biased susceptibility to trapping, the basis for this skew in sex ratio is unclear. Data on sex ratios of coyotes in the Northeast are sparse. Between 1979 and 1981 the sex ratio in New Brunswick and Nova Scotia was skewed towards males (60-65% male), while the sex ratio in New Hampshire was skewed towards females (39% male) (Moore and Millar 1984). The male-biased sex ratio continued throughout the 1980s in Nova Scotia (Parker 1995). The high proportion of males in the Atlantic Canada population may be a function of recent colonization and greater movement of males into vacant regions.

Few studies have examined the population densities of coyotes in the Northeast. Density in boreal forest of southeastern Québec are quite low - 0.02-0.03/km², suggesting that this habitat may be marginal for coyotes (Samson and Crête 1997). Density in mixed hardwood-coniferous forest in southeastern Québec is a bit higher (0.07/km²; Fortin 1995). These numbers are far lower than estimates from western and southern North America where densities may reach extremes of 1 to 3.9/km² (Knowlton 1972, Hein and Andelt 1995, Bourne 1991, Parker 1995), and the studies likely do not accurately represent densities elsewhere in the Northeast. For instance, Hilton (1986) reports a winter density in Maine of 0.57/km², and Parker (1995) suggests densities of 0.1-0.2/km² might be appropriate estimates for much of the Northeast. Recent annual harvests in Maine ranged between 1,222 and 1,647 individuals (about 1 per 48-65 km²), which was similar to harvested coyote

In agricultural regions the diets of coyotes may differ dramatically from that observed in forested sites

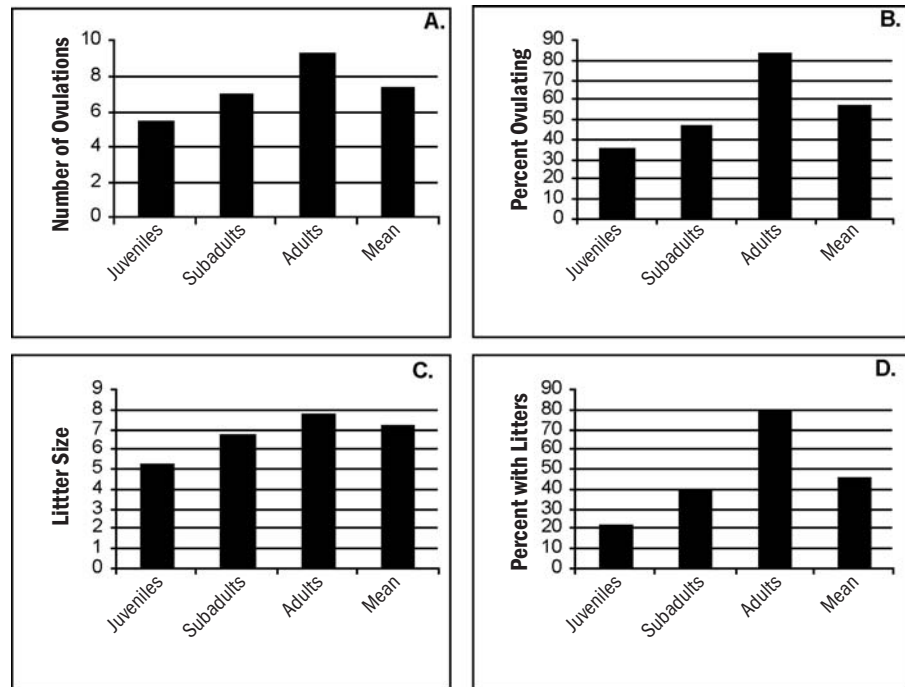


Figure 2. Measures of number of ovulations (A), percent of females ovulating (B), litter size (C), and percent of females producing litters (D) for a coyote population in southeastern Québec. Data from Jean and Bergeron (1984).

densities in states and provinces of the northern Great Plains and Great Basin (Voigt and Berg 1987, Jakubas 1997). Although some reports have suggested that coyote population densities have plateaued in some areas (Wolkomir and Wolkomir 1989, Patterson 1995), no robust study of the demographics of eastern coyote population has been carried out to support this argument.

The age structure of a coyote population is highly dependent on the extent of human exploitation in the region. In the Gaspé Peninsula of southeastern Québec, animals could live to be 14 years of age, but most adult males were <7 years old and most adult females were <5 years of age (Crête and Lemieux 1994). Also in southeastern Québec in a region with high removal pressures, an examination of >200 female carcasses provided by trappers and predator control personnel found that 84% were <3 years old, of which 63% were <1 year old (Jean and Bergeron 1984). Similarly, 86% of animals in Maine were < 3 years old (Lorenz 1978). In the southeastern Québec population, annual productivity was 3.1-3.2 pups per female. This high productivity may have been a response to heavy trapping resulting in large litter size, a population biased towards juveniles, and a high turnover rate (Jean and Bergeron 1984).

Understanding coyote dispersal behavior is critical for predicting population density and designing robust local management strategies. The best study of dispersal by juvenile coyotes in the northeast is Harrison's (1992; Harrison et al. 1991) work in Maine, in which 47 juvenile coyotes were radio-collared and followed between 1981 and 1984. Pups began to move short distances from the dens at 6-8 weeks of age, and the radius and rate of pup movement increased linearly with age. However, exploratory movements outside of the natal home range did not occur prior to actual dispersal. Most pups (86%) dis-

persed during their first year of life, and all individuals dispersed by age 1.5 yr.

The Maine study found no differences between males and females in rate, age or distance of dispersal (Harrison 1992, Harrison et al. 1991). This contrasts with results of studies at western localities (Nellis and Keith 1976, Robinson and Grand 1958, Windberg et al. 1985, Hibler 1977, Berg and Chesness 1978) which found a variety of sex biases in dispersal. In Maine dispersal commenced during late September, peaked in October-November, declined to zero during December-January, then peaked again during February-March (Harrison 1992). While water barriers deflected the movement and resulted in higher concentrations of dispersers along these barriers, dispersers generally moved along initial dispersal bearings and thereby maximized dispersal distance. Mean minimum dispersal distance for males (n=9) was 113 km, and for females (n=11) was 94 km. One female dispersed 342 km into Vermont, and a male traveled 308 km to New Hampshire (Harrison 1992). Long distance dispersal was also reported for a female trapped in northern New York which was hit by a car 320 km southeast in New Hampshire (Kendrot 1998).

To what extent Harrison's study populations are representative of those found elsewhere in the Northeast is unclear. It is possible that low food densities at the Maine sites may have decreased the possibility of delayed dispersal and pack formation within the natal home range. Nonetheless, as Harrison (1992) notes, this long-distance dispersal behavior will likely confound attempts to manage local coyote populations, as removed animals will quickly be replaced by dispersers. Transient individuals can make up a significant portion of a population (e.g. 40% for a population in decline in New Mexico; Windberg et al. 1997), but studies quantifying the territorial:transient ratio have not occurred in the Northeast. In addition, the extent of population exploitation can significantly influence the likelihood of dispersal (Davison 1981), but this too has not been examined in the Northeast.

Mortality rates of coyotes in the Northeast are not well documented, and where rates are available human-induced mortality is extremely important. For instance, Major (1983) found that all mortality (n = 12) in western Maine was due to trapping, shooting, and collisions with automobiles. Survival of dispersers (age 0.5-1.5 yr.) in Maine was lower (0.47) than of residents (0.74) (Harrison 1992). In northern New York, annual survival rates at a site with road densities of 1.51/km² and with 44% of the habitat under agriculture were lower (0.24) than at an adjoining site (annual survival = 0.64) with lower road densities (1.02/km²) and 16.5 % of the area under agriculture. Of 16 known coyote deaths, causes of mortality included hunting and shooting (n=9), trapping (n=3), vehicle collisions (n=2), and "natural" causes (n=2) (Kendrot 1998). These high rates of human-caused mortality are typical of rates from populations in western North America (Voigt and Berg 1987). It is unclear whether intraspecific agonism is a significant cause of mortality as has been documented for wolves. There is, however, one report of a solitary male coyote being killed by three pack members in the Adirondacks (Okoniewski 1982).

The diseases and parasites of coyotes in the Northeast are little studied, and thus the ecology and epidemiology of coyote-parasite interactions are poorly understood in the region. This is unfortunate, as disease is an important issue for wildlife management and conservation (Funk et al. 2001). Much of what

Understanding coyote dispersal behavior is critical for predicting population density and designing robust local management strategies

Long-distance dispersal behavior will likely confound attempts to manage local coyote populations, as removed animals will quickly be replaced by dispersers

we know about the parasites of coyotes comes from the western United States (reviewed by Gier et al. 1978, Pence and Custer 1981, Parker 1995, Pence 1995), and detailed epidemiological studies of rabies and sarcoptic mange epizootics in coyotes have been conducted in Texas (Clark et al. 1994, Pence and Windberg 1994). Surveys of the viral and bacterial diseases of coyotes have been performed in Yellowstone National Park (Gese et al. 1997). Coyotes were found to have high prevalence of canine parvovirus, canine distemper, canine infectious hepatitis, and several other infectious pathogens, which the authors felt might represent a threat to the long-term persistence of the Yellowstone wolf population. Diseases of coyotes in the Northeast may similarly represent a threat to any successful wolf recovery. Spill-over of pathogens from a coyote reservoir into other rarer species may also be an issue worthy of examination.

Micro and macroparasite surveys have not been carried out in the Northeast, and thus only a few species have been definitively identified, although many others are likely to occur. For instance, ova of five endoparasite species were identified from feces in southern Pennsylvania: *Capillaria aerophila*, *Uncinaria stenocephala*, *Ancylostoma* sp., *Toxascaris leonia*, and *Isospora* sp. (Bixel 1995). It is likely that parasite surveys in the Northeast would also identify several of these species. Of diseases of more direct concern to humans and domestic carnivores, canine distemper virus was identified in a coyote in Cape Breton Island (Parker 1995), and four of 244 coyotes (1.6%) necropsied in New York between 1970 and 1982 were diagnosed with the virus (Okoniewski and Stone 1983). However, viral epizootics of distemper or rabies within northeastern coyotes have not been identified, and less than 0.4% of rabies cases in Ontario (1961-1969) involved coyotes (Johnston and Beaugard 1969).

Of macroparasites of concern for humans, *Toxoplasma gondii* antibodies were identified in 59% of 222 coyote sera samples from coyotes in Indiana, Kentucky, Michigan and Ohio (Dubey et al. 1999). Therefore there is a high possibility that the parasite also occurs among coyotes in the Northeast. The cestode *Echinococcus granulosus*, for which humans may also serve as accidental hosts, was identified in 0.5% of 339 coyotes examined in Ontario compared to approximately 20% of 520 wolves examined (Freeman et al. 1961). Its occurrence in northeastern coyotes is therefore likely rare, although this has not been definitively shown, and the Freeman et al. study occurred early in the process of coyote range expansion into the Northeast. Canine heartworm, *Dirofilaria immitis*, infections were found in 4.7% of coyotes in New York, with a higher incidence in counties bordering the Hudson River (Monson et al. 1973, Okoniewski and Stone 1983).

Ectoparasites such as ticks (e.g. *Dermacentor variabilis*, *Rhinocephalus sanguineus*) and fleas (*Pulex simulens*) are likely to be common on northeastern coyotes (Parker 1995, Gier et al. 1978), but their ecological impact is unclear. Of particular interest is sarcoptic mange (*Sarcoptes scabiei*) which can cause severe population declines in canids (Funk et al. 2001). In coyotes, sarcoptic mange may be enzootic or epizootic, but may only cause compensatory mortality (Pence and Windberg 1994), although ecological studies in the northeast have not been carried out to support this. Mange is also important because while the varieties of *S. scabiei* are highly specialized to their hosts, spill-over

from heavily infected canids to accidental hosts such as felids has been documented and may constitute a conservation threat for other carnivore populations. In the Northeast, prevalence of mange has been examined in New York, where 34% of necropsied coyotes ($n = 244$) were positive, and mange was the immediate cause of death of 3% of individual (Okoniewski and Stone 1983). Mange can sometimes be a contributing factor in the mortality of individual canids. For instance, Kendrot (1998) reported the death of one coyote due to pneumonia, possibly exacerbated by a heavy lungworm (*Capillaria aerophila*) infestation and a moderate sarcoptic mange infection. Mange has also been reported in Vermont coyotes (Person and Hirth 1991).

Factors that limit the numbers of top predators are usually unknown, and coyotes are no exception. In different regions coyotes may be limited by food availability, predation by wolves, human persecution, and disease. In general, however, it appears that coyote abundance is determined primarily by food availability as mediated by behavioral characteristics such as social dominance hierarchies and territoriality (Knowlton and Stoddart 1983, Knowlton and Gese 1995). In the Northeast there are few studies identifying primary causes of population fluctuations. Crête and Lemieux (1994) reported that coyotes on the Gaspé Peninsula in Québec declined following a decrease in the deer population.

Throughout the Northeast, there is no limit on the numbers of coyotes that may be taken during hunting and trapping seasons, and several states and provinces have open seasons on coyotes (Ray 2000). A clear understanding of the demographics of coyote populations in the Northeast is critical, especially where predator control or coyote hunting programs are under consideration. Because coyotes may be strongly density-dependent breeders, the enactment or extension of hunting seasons for coyotes or the commencement of predator control programs may trigger rapid rebounds in population size, at considerable expense. Theoretical models indicate that without sustained efforts to control coyotes, control efforts are likely to be unsuccessful in the long run, and may even stimulate growth in the coyote population (Knowlton 1972, Connolly and Longhurst 1975, Connolly 1978, Sterling et al. 1983). For instance, litter size in Texas varied with the intensity of control, with females inhabiting areas of light predator control having 2.8-4.2 uterine swellings, while individuals under intensive control had 6.2-8.9 swellings (Knowlton 1972). In control areas in the western United States, counts of fetuses or placental scars reached extremes of 14-17, suggesting compensatory reproduction (Voigt and Berg 1987). Clark and Fritzell (1992) reported that changes in total reproductive outputs is primarily a result of changes in yearly pregnancy rates and the survival of young cubs. Sex ratios and recruitment rates may also change in populations subject to intense hunting pressures and coyote control efforts (Berg and Chesness 1978, Davison 1991, Pyrah 1984, Crabtree and Sheldon 1999, Stephenson and Kennedy 1993). Litter size, juvenile survival, immigration and emigration, and the fraction of females breeding are also associated with population density as a function of food availability (Knowlton and Gese 1995), and determining the relative importance of food abundance, population density and the tangential influences of predator control is difficult. Nonetheless, similar changes in the reproductive biology of other canid species have been reported (Harris and Smith 1987, Hersteinsson 1992, Geffen et al. 1996), so there is

Factors that limit the numbers of top predators are usually unknown, and coyotes are no exception

reason to believe that such effects would occur in coyotes from eastern North America should human-associated mortality increase dramatically.

These demographic studies imply that hunting and predator control programs have limited success in reducing coyote populations, and may actually increase coyote population densities by lowering the mean age of reproduction, increasing litter size, decreasing dispersal, creating a sink for transient individuals that reach the region, and decreasing natural mortality rates. However, there is considerable controversy among coyote researchers as to both the impact of control programs on the demographics of these predators, and the possible mechanisms by which coyote populations are able to rapidly recover from a local population reduction (Knowlton and Gese 1995, Crabtree and Sheldon 1999).

Habitat Use by Northeastern Coyotes

Across North America, coyote home range size varies as a function of food availability, with animals in more northern latitudes having larger range sizes than more southern animals (Gompper and Gittleman 1991). On a regional scale, resident coyotes occupy stable home ranges that vary seasonally in the proportion of home range that is used. In eastern Maine, Caturano (1983) monitored home range use of three packs. Mean home ranges (males = 51.7 km²; females = 48.2 km²) did not differ in size, shape or location between breeding pairs in each pack. Core areas where at least 50% of radiotelemetry locations were observed covered <25% of the home range. Female range use increased with nursing and later pup-raising. Males increased their ranges during gestation while females decreased their range (Harrison 1983, Harrison and Gilbert 1985). In western Maine, home range sizes (n = 5) averaged 43.3 km² (Major and Sherburne 1987).

In Nova Scotia, minimum annual sizes of three breeding territories were 93.8, 62.7, and 39.5 km² (Patterson 1995). In the central Adirondacks of central New York, home range sizes were larger still, averaging 112.8 km², but home ranges based on biological seasons averaged just 38.8 km². Home range overlap between packs was minimal based on seasonal ranges (Brundige 1993). In northern New York in a region where agriculture was a major land use, home range sizes were smaller; non-denning season home ranges averaged 18.9 km² and 14.4 km² for male and female coyotes, respectively (Kendrot 1998). Agricultural habitat may thus be higher quality for coyotes than forested habitat. In support of this, Person and Hirth (1991) reported coyote home ranges of 18.7 km² and 17.1 km² for males and females, respectively, in an agricultural region of Vermont. In southeastern Québec, Tremblay et al (1998) found that during periods of den attendance and pup rearing (May – September) forest-inhabiting coyotes had home ranges more than 2-3 times larger than coyotes in adjoining rural habitat.

Coyote habitat use varies seasonally. In eastern Maine, Caturano (1983) found that 94% of relocations of radiocollared animals occurred within forest cover. Litvaitis and Harrison (1989) found that in spring coyotes used open areas more than expected and mixed-wood cover and bog area less than expected. In summer and fall coyotes used softwood areas more than expected and

mixed-wood cover less than expected. In winter coyotes used hardwood areas more than expected and softwood cover and bog areas less than expected. Looking at habitat use as a function of biological season, 84% of locations during the pair-bonding and breeding season were evenly divided between softwood and mixed-wood habitats, with mixed-wood habitat used more than expected by chance. Gestation, nursing and subsequent pup-raising took place primarily in softwood habitats in a proportion also greater than expected by chance. Relatively little activity occurred in hardwood, barren and heath habitat (Caturano 1983). In western Maine, coyotes selected predominantly coniferous forest stands. Frozen lakes and ericaceous bogs were also used extensively. Clearcut areas were also used during the summer (Major and Sherburne 1987, Major 1983).

In the Adirondacks, seasonal habitat use reflected habitat availability, with preferences shown for open habitats such as beaver meadows and frozen lakes during winter. Preference was also shown for habitats with dense understories and midstories. These preferences may reflect food acquisition and reproductive requirements (Brundige 1993).

In the Champlain Valley of Vermont, coyotes preferred hardwood forest during winter and spring, and farmland during summer and fall (Person and Hirth 1991). A comparison of habitat use at two sites in northern New York, one dominated by agriculture (44%) and with higher road densities and the other less developed (17% agriculture), coyotes preferred forested habitats and avoided agricultural and urban areas. Coyotes also excluded primary roads from their home range, and excluded secondary roads from areas of core use (Kendrot 1998). Nonetheless, vehicle collisions did cause 12.5 % (n = 16) of mortality at the study site. In western regions the availability of road-killed animal carcasses has been found to increase coyotes use of roads and associated traffic mortality (Found 1996). In Maine, Major (1983) also found that coyotes used roads to travel and to demarcate boundaries.

Aside from Major and Sherburne's (1987) report of summer use of clearcuts, there has been little study in the Northeast of coyote habitat use as a function of extractive logging. How coyotes use suburban and urban areas is also poorly understood. Person and Hirth (1991) found that near Burlington and Middlebury, Vermont, several family groups successfully raised litters near (< 800 m) housing developments. These coyotes did not use these developments more frequently than expected, however. That is, the coyotes lived near human development but actually avoided buildings.

The Coyote and Community Ecology

Coyotes are direct and indirect competitors with a wide array of species. It is therefore worth examining how the presence of coyotes in the Northeast has influenced, or in the future may influence, abundances and distributions of other species, including species of conservation concern. For example, it is unclear whether the presence of coyotes has significant influences on wolf population recovery rates. Coyotes and wolves are well-documented interference competitors (Fuller and Keith 1981, Berg and Chesness 1978, Litvaitis 1992, Peterson 1996, Crabtree and Sheldon 1999, Carbyn 1982, Johnson et al. 1996,

Demographic studies imply that hunting and predator control programs have limited success in reducing coyote populations

Few studies in the Northeast have examined coyote use of habitat as a function of extractive logging. Use of suburban and urban areas is also poorly understood

Paquet 1991, Thurber et al. 1992). Where wolves have been reintroduced or have naturally recolonized, coyote densities have declined, and coyote habitat use, group size, body size and diet have changed (Arjo 1998, Krefting 1969, Crabtree and Sheldon 1999, Finkel 1999).

Just as wolves in some regions limit coyotes, coyotes are in turn known to limit smaller canid numbers in many parts of North America (Johnson et al. 1996; Cypher and Spencer 1998; Ralls and White 1995). This has been shown in the Northeast. For instance, concurrent with the establishment of coyotes in the Hudson Highlands of southeastern New York was a decline in fox densities and the elimination of feral dogs inhabiting some forested regions (Brady 1994). In Maine the red fox (*Vulpes vulpes*) harvest decreased as coyotes became established (Halpin and Bissonette 1986). Field studies in eastern and western Maine and Québec found that red fox home ranges were usually located outside the boundaries of coyote territories, suggesting interference competition between the species (Major and Sherburne 1987, Harrison et al. 1989, Fortin 1995). Major and Sherburne (1987) never captured a red fox within the core area of a coyote territory in over 7000 trap nights covering a four year period. Coyotes and red foxes also share prey such as snowshoe hares, and although foxes may benefit by feeding on deer carcasses killed by coyotes, the dietary niche overlap may be high enough to result in exploitation competition for resources (Dibello et al. 1990).

In contrast to their findings for coyote-red fox interactions, Major and Sherburne (1987) found no evidence for interference competition between coyotes and bobcats. Litvaitis and Harrison (1989) also found no evidence of avoidance or attraction behavior between neighboring radiocollared bobcats and coyotes, and home ranges and activity patterns overlapped extensively. However, exploitation competition for food, particularly snowshoe hares, may exist (Dibello et al. 1990, Litvaitis and Harrison 1989). Litvaitis and Harrison speculated that coyotes had reduced the carrying capacity of bobcats in eastern Maine by reducing the availability of prey during periods where the prey base was most limited, and that the colonization of Maine by coyotes resulted in a diet shift by bobcats to fewer deer and red squirrels and more snowshoe hare. In addition, between 1974 and 1985 the harvest of bobcat in Maine declined 73% while the harvest of coyotes rose sharply (Litvaitis and Harrison 1989, Hilton 1986). This pattern also occurred in the central Adirondacks (Fox 1990). Litvaitis and Harrison (1989) suggested that this may be evidence of exploitation competition between the species. Many factors are unclear, however. The effects of human harvest were not known, the deer population also declined, the length of the bobcat harvest season was reduced, and several severe winters occurred during this period (Major 1983, Litvaitis and Harrison 1989, Dibello et al. 1990). Litvaitis and Harrison (1989) proposed that because bobcats are more efficient predators in microhabitats with dense understories and abundant snowshoe hare populations, they will not be completely displaced. Rather, bobcat numbers may stabilize at a new equilibrium below that which occurred in pre-coyote times. This hypothesis deserves additional attention, and the interactions of coyote and bobcat populations remain unresolved.

The interaction between coyotes and other mesocarnivores is less studied. One study in Mississippi hypothesized that gray fox (*Urocyon cinereoargen-*

teus) may be excluded from better habitat by coyotes (Lovell 1996). However, this remains to be demonstrated unambiguously; Edwards (1996) found no evidence of such displacement, and only inconclusive evidence for coyote-modified patterns of habitat use. Coyote-gray fox interactions have not been examined in the Northeast. Coyotes may also locally influence raccoon populations. On Mount Desert Island, Maine raccoons are the most important component of the autumn diet of coyotes (O'Connell et al. 1992). The killing of raccoons was also reported in winter in Québec (Bergeron and Demers 1981). In the case of lynx, exploitation competition may occur, as both species rely heavily on snowshoe hares where they are sympatric and few alternative prey species exist (O'Donoghue et al. 1997). However, Fortin (1995) suggested that the lynx has not been severely affected by coyote colonization because of the presence of preferred lynx habitat, the inefficiency of coyotes in capturing snowshoe hares in deep snow, and the availability of alternative food sources for coyotes.

Virtually no data exist on the interactions of coyotes and martens (*Martes americana*) and fishers (*M. pennanti*). Fishers have been reported to visit deer carcasses killed by coyotes (Major and Sherburne 1987). Litvaitis (1992) has suggested that a coyote-associated reduction in numbers of bobcats and foxes may release marten and fisher populations, but data to support this do not exist.

The presence of coyotes may have a variety of indirect effects on non-prey animals and plants. For instance, Chambers (1987) noted that in the Adirondacks, eagles (*Aquila chrysaetos* and *Haliaeetus leucocephalus*) and ravens (*Corvus corax*) scavenge the carcasses of deer killed by coyotes. He notes that breeding populations of ravens reestablished in the Adirondacks and increased "in parallel with increased coyote numbers and an apparent increase in predation on deer by coyotes". Whitaker and Hamilton (1998) suggest that because coyote limit red fox populations and red foxes limit long-tailed weasel populations, which in turn exclude least weasels (*Mustela nivalis*) from areas of high resource value, coyotes may be indirectly controlling weasel densities. Proulx et al. (1994) observed a yearling black bear (*Ursus americanus*) give way to an adult coyote, although the implications of this are unclear and there is no evidence that coyotes influence black bear populations. For the most part, however, little work on the indirect effects of coyotes has been carried out in the Northeast. Elsewhere in North America, altered coyote densities have been associated with:

- Increased nest success of ducks due to interference competition with and predation on red foxes (Sovada 1993, Sovada et al. 1995).
- Increased diversity of songbird and rodent communities due to predation on domestic cats (Crooks and Soulé 1999).
- Increased nest success of ground-nesting song sparrows (*Melospiza melodia*) due to predation on raccoons (Rogers and Caro 1998).
- Decreased rodent species diversity and biomass, and increased abundances of other mesocarnivores following experimental reduction of coyote populations by 48% (Henke and Bryant 1999).
- Declines in burrowing owl (*Athene cunicularia*), partridge (*Perdix perdix*), and grouse (*Tympanuchus phasianellus*) populations following a decline in coyote and increase in red fox populations (Finley 1996).

Little work on the indirect effects of coyotes has been carried out in the Northeast

RESEARCH RECOMMENDATIONS

It is clear that the coyote is now an important predator throughout northeastern North America. While studies carried out to date have revealed a great deal of information on the natural history and ecology of coyotes in the region, there are also several significant gaps in our knowledge base, and these gaps make it difficult to make informed conservation decisions. In particular, four aspects of coyote ecology are suggested as priorities for future research: coyote demographics, the role of coyotes as keystone predators, the diseases of coyotes, and the importance of wolf genotype introgression into the coyote population.

The demographics and growth rates of the northeastern coyote populations.

Coyote populations have increased throughout the Northeast. Unclear is whether population growth has peaked or if population sizes will continue to increase. Until this issue is resolved, it will be difficult to assess how common coyote-human interactions will become, and what impact coyotes will have on other species.

The role of northeastern coyotes in structuring communities.

Coyotes have the potential to significantly influence the population sizes of a broad array of species, some of which may be of significant concern to conservation and wildlife biologists. How community structure will change as a function of the colonization of the Northeast by coyotes has not been adequately addressed.

The important parasites and diseases of northeastern coyotes.

An in-depth understanding of the parasites and diseases of northeastern coyotes does not exist. This work should be a high priority, if only because the coyote population may act as a reservoir for a variety of diseases that may negatively influence other carnivore populations.

The importance of wolf-coyote hybridization in the Northeast.

Coyotes are known to hybridize with wolves in the Midwest, and coyote genotypes have been identified within wolf populations. Whether the introgression of wolf genes into the coyote population has also occurred, and whether this is a significant factor in understanding the biology and ecology of coyotes in the Northeast has not been adequately addressed. This is especially important in light of the possible future return of wolves to the Northeast.

Finally, it should be noted that most studies of coyotes in the Northeast have been conducted at just a few sites or for relatively brief periods. Regional differences and temporal variation therefore remain poorly understood. In particular, most studies have been in rural, forested regions. The ecology of coyote populations inhabiting areas with higher human densities, such as suburban and coastal regions, is unknown.

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