Wolf Reintroduction Feasibility in the Adirondack Park

Prepared for the Adirondack Citizens
Advisory Committee on the Feasibility
of Wolf Reintroduction

by
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INTRODUCTION

It has been commonly reported that gray wolves (*Canis lupus*) as well as other predators like panthers (*Felis concolor*) and lynx (*Lynx canadensis*) once lived throughout the northeastern U.S. including what is today the Adirondack Park. Extirpation of these summit predators closely followed European settlement (see Schneider 1997). As a result of an active bounty system, the last wolf was believed to have been killed in Upstate New York during the mid 1890s.

In recent years, gray wolf recovery (both natural and human-directed) has been successful in a number of locations throughout North America -- most successfully in the Upper Great Lakes region of the U.S. (see Fuller 1995). A second population of gray wolves in the eastern U.S. outside the Minnesota population has been expressed as a goal for gray wolf recovery in the U.S. by federal agencies (see U.S. Fish and Wildlife Service 1992), and the Northeast has been identified as a potential region to support a viable population of wolves. In addition to northern sections of Maine, New Hampshire, and Vermont, the AP has been identified as potentially supportive of gray wolves (see Mladenoff and Sickley 1998).

This study was by the Adirondack Park Citizens Action Committee organized by Defenders of Wildlife to examine the issue of gray wolf recovery in the Adirondack Park (from now on referred to as simply AP). By combining what has been learned about wolf biology from numerous field studies with geographic information systems (GIS), we addressed the issue of gray wolf reintroduction feasibility in the AP. In addition to developing wolf habitat suitability and connectivity models, we examined the important genetics questions pertinent to wolves in the AP.

GRAY WOLF NATURAL HISTORY

Historically, the primary limiting factor for gray wolves has not been habitat degradation, but direct persecution through hunting, trapping, and predator control programs. As public antipredator sentiment and the economic importance of the livestock industry diminishes, wolves are well equipped biologically to recolonize what remains of their former range. Map-based regional conservation planning can help facilitate human-wolf coexistence by identifying areas where human development and high quality wolf habitat do not come in contact (Mladenoff et al. 1995, Boitani et al. 1997, Mladenoff et al. 1997). To predict what influence wolves would have on the biology of the Adirondacks requires a general understanding of wolf population dynamics, and the ecological relationships between wolves and their prey (primarily ungulates), scavengers, and other predators. The biology, of course, is strongly modified and often constrained by the historic and ongoing activities of humans on the landscape.

Wolf Population Dynamics

Wolf population dynamics are believed to be largely dictated by the per capita amount of prey, vulnerability of prey, and the degree of human exploitation (Keith 1983, Fuller 1989). The effect of food on wolf demography is mediated by social factors, including pack formation, territorial behavior, exclusive breeding, deferred reproduction, intraspecific aggression, dispersal, and by primary prey shifts (Packard and Mech 1980, Keith 1983, Paquet et al. 1996).

The wolf shows high levels of ecological resilience compared with other large carnivores due to the species' exceptional adaptability and favorable life history traits (Weaver et al. 1996). Wolves demonstrate the ability to alter their own social structure by altering pack structure (Chepko-Sade and Shields 1987), fertility levels, dispersal, and tolerance of other wolves in response to shifts in their own population densities. These social changes are usually precipitated by different levels of mortality within packs and regional prey abundances (Fritts and Mech 1981, Fuller 1989, Boyd et al. 1995, Weaver et al. 1996).

Unlike other large carnivores, wolves have a high capacity to replace their numbers because they reach sexual maturity at an early age and have large litters. This is one reason why wolves, in comparison with other large carnivores, have been able to withstand high levels of mortality. Because of this high reproductive capacity, one would expect wolves to outnumber other predators in a region, but population densities of wolves are usually far lower than population densities of other large carnivores (e.g., bears) occupying the same areas. There are several reasons for this: (1) wolves are easily displaced by human activities; (2) social animals are more susceptible to removal than solitary animals; (3) unlike bears, wolves are active throughout the year; (4) wolves occupy large home ranges, which increases exposure to humans; and (5) wolves often travel long distances, which increases exposure to humans. Wolves do not become casualties of management due to direct contact with humans as frequently as bears (wolves tend to avoid humans), but wolves are often sought out and killed because of predation on domesticated animals, predation on a preferred game species, or for sport.

Biologists usually define the home range of a wolf as an area within which it can meet all of its annual biological requirements. Seasonal feeding, security needs, unobstructed travel routes, denning sites, and the bearing and raising of young are all essential life history requirements. The manner in which habitats for these requirements are used and distributed influences home range size and local and regional population densities and distributions. Generally, wolves locate their home ranges in areas where adequate prey is available and human interference is minimized (Mladenoff et al. 1995). Wolves also use their home ranges in ways that maximize encounters with prey (Huggard 1993a,b). Home range selection by wolves is influenced by a number of important factors. Among them is topographic position, which has been shown to influence selection of home ranges as well as intra- and interregional travel routes (Paquet et al. 1996). In mountainous areas, wolf use of valley bottoms and lower slopes during the winter months usually correspond to the presence of ungulate prey (Paquet et al. 1996, Boyd 1997). Notably, humans are attracted to these same areas for recreation and facility development such as highways and railroads.

In expanding populations, many wolves become dispersers. Wolves can disperse over hundreds of kilometers. Mean dispersal distances reported in published works varied from 65 to 154 km (40-95 miles) for males and from 65 to 123 km (40-76 miles) for females (Fritts and Mech 1981, Peterson et al. 1984, Fuller 1989, Gese and Mech 1991, Wydeven et al. 1995, Ballard et al. 1987, Boyd 1997). The longest dispersal distance recorded for a wolf is 840 km (520 miles) (Boyd et al. 1995). Colonizing wolves have been known to move in areas greater than 100,000 km^2 (Paquet unpublished data).

Dispersal is a critical element of colonization (Gese and Mech 1991, Boyd et al. 1995). It also may be an important process in gene flow (Forbes and Boyd 1996), social organization, and metapopulation persistence. Because of their capacity for long range dispersal, the typical genetic threats associated with small population sizes are of less concern for wolves than for other animals (Fritts and Carbyn 1995, Boyd et al. 1996, Forbes and Boyd 1997). Both sexes disperse, resulting in higher effective population size (N_e) (Chepko-Sade et al. 1987, Forbes and Boyd 1997). Dispersal dynamics are important at within-population and metapopulation scales (Haight et al. 1998).

Wolf-Prey Interactions

As stated earlier, wolf numbers are closely linked to population levels of their ungulate prey (Keith 1983, Messier 1985, Fuller 1989). Because wolves rely primarily on ungulates for food, survival of wolves in the Adirondacks will depend on protection of habitat for deer and to a lesser degree moose and beaver. Viable, well-distributed wolf populations are always linked to abundant, stable, and available prey populations.

In environments where factors such as weather and hunting reduce prey populations substantially, predation by wolves can inhibit the recovery of prey populations for long periods (Gasaway et al. 1983). In a multiprey system, the stability (or equilibrium) of ungulate prey and wolf populations seems to depend on a variety of factors, including the wolf predation rate, the number of ungulates killed by hunters, the ratio of ungulates to wolves, and the population growth rate of different ungulate species (Carbyn 1982, Paquet 1993, Paquet et al. 1996, Weaver 1994).

Many studies have emphasized the direct effects (e.g., prey mortality) wolves have on the population dynamics of their ungulate prey (Carbyn 1974, Carbyn 1983, Gasaway et al. 1983, Messier 1994, Messier and Crete 1985, Peterson et al. 1984, Ballard et al. 1987, Boutin 1992, and others). However, predation also can profoundly affect the behavior of prey, including use of habitat, time of activity, foraging mode, diet, mating systems, and life histories. Accordingly, several studies describe the influence wolves have on movements, distribution, and habitat selection of caribou, moose, and white-tailed deer (Mech 1977a, Ballard et al. 1987, Nelson and Mech 1981, Messier and Barrette 1985, Messier 1994).

Without human disturbance, wolf densities generally reflect the dependency on ungulate prey species (Keith 1983). Wolves can increase the rate at which they acquire resources by seeking out areas with dense concentrations of prey (Huggard 1991, Weaver 1994). Prey, in turn, can lower their expected mortality rate by preferentially residing in areas with few or no wolves.

Several studies have suggested that ungulate prey seek out predator-free refugia to avoid predation by wolves (Mech 1977, Paquet 1993). Wolf predation in the Superior National Forest (SNF) of northern Minnesota was found to affect deer distributions within wolf territories (Mech 1977). Densities were greater along edges of territories where predation was thought to be less. However, recent studies in Banff National Park, Alberta support an alternative explanation that ungulate productivity is higher in areas without wolves, which results in higher prey numbers in predator-free zones (Paquet et al. 1996). This phenomenon may be pertinent to the Adirondack Park region.

Wolf packs may react to changing conditions in varying ways, depending on the location of their territories in relation to other packs and prey distribution. If packs have lower prey densities within their territories, they may exploit territories more intensely. Territory size is more closely correlated with pack size than with prey density (Messier 1985a, Peterson et al. 1984), and in areas of higher prey density, pack sizes increase (Messier 1985b). Messier’s (1985b) data indicate that between 0.2 and 0.4 moose/km^2, territory area per wolf is independent of moose abundance. This may be achieved by: (1) persevering in each prey attack, (2) using carcasses thoroughly, (3) feeding on alternative and possibly second-choice food resources such as beaver (Messier and Crete 1985), and (4) patrolling their territory more intensely (Messier 1985b). Messier, in his study area in southeastern Quebec, found daily distances of Low Prey packs were on average either greater than (in summer) or equal to (in winter) daily distances of High Prey packs. The territory size, however, was approximately 35% smaller in the Low Prey area, suggesting that wolves were searching each unit area with greater intensity in both seasons.

Miller (1976) reported that wolf-killed caribou were not randomly distributed, and therefore certain sites must give wolves an advantage over their prey. Peterson and Woolington (1984) found most wolf-killed moose on the Kenai Peninsula in old burns, often associated with small stands of timber remaining in the burn. Stephens and Page (1987) concluded that moose seek conifer cover and its associated structure to reduce attack rates by wolves. In theory, changes in habitat composition and distribution can have a profound effect on ungulate densities and distributions, and therefore wolf spatial distribution.

Antipredator behaviors of ungulates may substantially influence habitat selection by wolves and prey. The natural dispersion of ungulate prey over many patches, and spatial variation in population growth, may lead to a “source-sink” population structure for wolves and their prey (Huggard 1991, Paquet et al. 1996). Human activities also may alter these spatial dynamics in unanticipated and adverse ways. For example, deer and moose are highly vulnerable to wolf predation in fragmented habitats created by clearcuts (ADFG). Fragmented landscapes create greater edge area and potentially less and/or inaccessible escape cover. In some instances, wolves may be deprived access (spatial isolation) to ungulate prey because of human created impediments to movement (e.g., town sites, highways), which results in artificial predator-free zones (Paquet 1993, Paquet et al. 1996). Conversely, activities such as cross-country skiing or keeping roads snow-free may provide wolves access to refugia traditionally used by ungulates to avoid predators (Paquet 1993, Paquet et al. 1996). These changes can lead to different intrinsic rates of growth for ungulates using different habitat patches. Over time, the distribution, density, and long-term demographic patterns of ungulates may depart from the “undisturbed norm.”

The human induced change in predator-prey relationships may also affect species other than wolves and their prey. Disruption of top predators can affect interspecific associations by disrupting relationships within food webs. This, in turn, may cause unanticipated ripple effects in populations of other species (Paine 1966, 1969, 1980; Terborgh and Winter 1980, Frankel and Soulé 1981, Wilcox and Murphy 1985, Wilcove et al. 1986), which markedly alter the diversity and composition of a community (Paine 1966). Multispecies effects often occur when changes in a third species mediate the effect of one species on a second species (or analogous higher-order interactions). For example, a wolf can affect a grizzly bear by reducing the availability of a limiting resource (possibly an ungulate). Also a secondary carnivore such as a coyote (*C. latrans*) can affect the degree to which a herbivore's lifestyle is influenced by a primary carnivore such as a wolf. Ecologists have only begun to develop theory that attempts to explain the coexistence of prey in terms of predator-influenced niches ("enemy-free space").

As noted above, many indirect effects of predation on community structure and diversity have been proposed. Research has documented differences within systems from which large predators have been removed or are missing (Soulé et al. 1988, Terborgh 1988). A recent study on Isle Royale, Michigan found strong evidence of top-down control of a food chain by wolves. Growth rates of balsam fir (*Abies balsamea*) were regulated by moose density, which in turn was controlled by wolf predation (McLaren and Peterson 1994). When the wolf population declined for any reason, moose reached high densities and suppressed fir growth. This top-down “trophic cascade” regulation is apparently replaced by bottom-up influences only when stand-replacing disturbances such as fire or large windstorms occur at times when moose density is already low (McLaren and Peterson 1994).

Tolerance to Human Disturbance

If we are to judge the effects of human influence, then we must know the uninfluenced norms and ranges. Information on wolf responses to natural causes of population fluctuations is lacking, and influence by humans is therefore imperfectly understood. The specific conditions in which wolves are “disturbed” (i.e., distribution, movements, survival, or fertility are impaired) are believed to be highly variable. The extent and intensity of disturbance appear to vary with the environmental and social context and the individual animal. Though many large carnivores are sensitive to human predation and harassment (Thiel 1985, Mattson et al. 1987, McLellan and Shackleton 1988, Knight et al. 1988, Mattson and Knight 1991 a,b, Thurber et al. 1994), we have limited empirical information on tolerance to indirect human disturbance. However, many researchers believe that the response of species to a particular disturbance depends largely on disturbance-history. Disturbance-history is a critical concept in understanding the behavior of long-lived animals that learn through social transmission (Curatolo and Murphy 1986, S. Minta pers. commun.). New disturbances, with established background disturbance, may surpass the level of habituation or innate behavioral plasticity that allows the animal to cope with disruption.

To complicate an already complex situation further, it is unlikely that all carnivore species or individuals within species react equally to human induced change. Species adapted to mature forests or large tracts of undisturbed land, such as grizzly bears or wolves, may be especially vulnerable to loss of habitat and human disturbance.

We can group human impacts into influences on wolf habitat and populations. Habitat disturbance can be short or long term and can include direct loss of habitat (i.e., vegetation removal and change) or indirect loss because of incompatible activities. Direct habitat loss does not include the loss of habitat due to temporal or spatial alienation (sensory disturbance) or from fragmentation of habitat. Indirect losses will occur due to habitat alienation, where animals abandon habitat because of nearby disturbances or are spatially isolated from using them because of impediments to movements. Changes in population can occur directly through alterations in habitat and indirectly because of disturbing activities.

The major effects of human induced changes are, in order of decreasing importance, physical loss of habitat, fragmentation of habitat, isolation of habitat, alienation of habitat, alteration of habitat, changes in original ratios of habitat, and changes in juxtaposition of habitats. These effects combine to have local and population level influences by altering the composition of biological communities upon which wolves are dependent, restricting movements, reducing foraging opportunities, and limiting access to prey. Obstructing movements also increases the vulnerability of wolves to other disturbances as they attempt to learn new travel routes.

The degree to which human activities disrupt wolves reflects the type and extent of disturbance, which interacts with the natural environment to affect environmental quality. In mountainous landscapes such as the Adirondacks, wildlife often responds markedly to disturbances that occur at small spatial scales. This is because the topography amplifies the effects of disturbances by concentrating activities of humans and wildlife into valley bottoms. The forced convergence of activities limits spatially the range of options wildlife has for coping with disruption, reducing resilience to human disturbance (Weaver et al. 1996).

Habitat selection by wolves is a complex interaction of physiography, prey availability, security from harassment, population density, and disturbance history, and each facet is subject to reliable modeling provided the data needed to examine them are available. Seasonality is also an important consideration in examining wolf habitat effectiveness. In summer, wolves need to den and raise their young, whereas in winter, wolves must remain active and survive harsh conditions.

THE LATEST GENETICS STORY

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Genetic Characterization and Taxonomic Description of New York Canids

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HISTORIC NEW YORK WOLVES

Wolves existed within what is now New York State before and during early European settlement. However, the distribution of canids has changed dramatically within the last two hundred years. De Kay (1842) described the common American gray wolf (*Lupus occidentalis*) inhabiting New York State:

Characteristics: Color various from white to black, usually greyish. Space between ears greater than their height. Feet broad. Neck and tail with bushy hair.

DeKay further described two varieties of the American wolf:

Var. a. *Grey Wolf*. White or greyish in winter, in summer it has short reddish hairs. This is the most common kind.

Var. b. *Black Wolf*. Entirely black, more bulky and powerful than the preceding. Very rare.

The predominant prey of the most common wolf (Var. a.) was described as white-tailed deer (*Odocoileus virginianus*). In the mid-1800s, the distribution of wolves in New York State was reduced to mountainous and wooded parts and the counties along the St. Lawrence. The reduction of wolf numbers in the 1800s resulted in the near or complete extirpation of wolves in the State. This was heavily influenced by bounties of $10-$20 per wolf.

Characteristics described by De Kay (1842) are consistent with two overlapping wolves: the eastern Canadian wolf (*C. lycaon*) as Var. a. and the gray wolf (*C. lupus*). The above taxonomic classifications are based on recent genetic research conducted at Trent and McMaster Universities. The new evidence suggests the need for a revision of canid taxonomy in eastern North America. Mitochondrial DNA (mtDNA) and microsatellite DNA analysis of the eastern Canadian wolf and the red wolf (*C. rufus*) indicated a close genetic relationship between these two wolves. Furthermore, the evolution of these two species appears independent of the gray wolf (Wilson et al. 1999 - see appended manuscript). Under this proposed evolutionary model, the progenitor of the gray wolf migrated to Eurasia 1-2 million years ago and subsequently returned to North America during the Pleistocene approximately 300,000 years ago. In addition to the genetic data, morphology and the fossil record support the close relationship of the eastern Canadian wolf and the red wolf. Perhaps the most important similarity between the proposed North American evolved wolves is their ability to hybridize with coyotes. Hybridization between wolves and coyotes appears limited to eastern North America, i.e. east of Minnesota and Manitoba, and under the proposed evolutionary history, represents the interbreeding of closely related sister taxa and not the hybridization of gray wolves and coyotes that diverged 1-2 million years ago. The recommended species name for the eastern Canadian wolf/red wolf is *C. lycaon*.

We tested this model by analyzing the genetic markers of wolves present in southeastern Canada and the northeastern U.S. before the arrival of coyotes into the area. The last reported wolf in New York was killed and mounted in 1893 (Adirondack Museum; Catalogue Number 79.10.1). This animal was described as follows:
Descriptors: Nat Hist 10
Provenance: Trapped by Reuben Cary, donor's grandfather
Description: WOLF- last gray wolf killed in Adks. Stuffed and mounted. Two tags on mount: "Gray Wolf/canis occidentalis Pick/ The last wolf killed in the Adirondacks. Shot near Brandeth Lake, Hamilton County November 10, 1893 by Reuben Cary. Loaned by General E. A. McAlpin." "This wolf was caught in a trap in the Clearing by Reuben Cary in November 1893." The above inscription was placed on the wolf when he was exhibited at the St. Louis World's Fair by the Forest Fish & Game Commission in 1903.
Dimensions: 27" at shoulder,
Condition: 52" nose to tail.

We analyzed a sample of hide from the 1893 wolf and identified a coyote-related mtDNA. Given the absence of coyotes in New York State in 1893, the coyote-related genetic marker is consistent with the evolution of a New World wolf more closely related to the coyote (*C. latrans*) than the gray wolf. Other genetic models of eastern canid history describe the hybridization of gray wolves (*C. lupus*) and coyotes (Lehman et al. 1991, Wayne and Lehman 1992, Roy et al. 1994, Roy et al. 1996). Under this model, eastern wolves, before the arrival of coyotes, should contain only a gray wolf (*C. lupus*) mtDNA. Coyote mtDNA would not have been introgressed into wolf populations until the expansion of coyotes into this region. Therefore, the genetic analysis of the 1893 historic wolf sample supports the existence of *C. lycaon*.

EASTERN COYOTES

The coyote (*Canis latrans*) has expanded its range extensively over the past 100 years, from southwestern U.S. (Great Plains) into northeastern U.S., southeastern Canada, the Great Lakes region, northern Quebec, Yukon, and Alaska. The cause of this expansion has been accredited to alterations in habitat previously occupied by wolves (*C. lupus*) (Nowak 1978). Following an almost 30-year period during which no wolves were known to occur in New York, a coyote-like animal was reported in the St. Lawrence Valley area in 1920. Reports of large coyote-like animals continued to increase in the early 1930s in Ontario and as early as 1936 in Maine. Coyotes were considered common in the Adirondacks, New York during the 1950s. By the 1970s these animals had extended their range across southeastern Canada and the northeastern states, migrating to Newfoundland in 1987 (Moore and Parker 1992).

The larger body size of the “eastern coyote” differentiates it from the western coyote; i.e. skull measurements of eastern coyotes are intermediate between western coyotes and gray wolves (Lawrence and Bossart 1975, Nowak 1979). In addition, the behavior of eastern coyotes has been described as more aggressive than western coyotes (Silver and Silver 1969). White-tailed deer constitute as much as 75-90% the eastern coyote’s (Chambers 1975, Messier et al. 1996).

Four main hypotheses have been proposed to explain the larger morphology and intermediate wolf-like characteristics of the eastern coyote. First, the eastern coyote represents a “coydog” resulting from dog (*C. l. domesticus*) and coyote interbreeding (Silver and Silver 1969, Mengel 1971, Lawrence and Bossart 1975). Second, the eastern coyote has undergone selection for a larger body size as an adaptive response to larger prey, specifically white-tailed deer (Kolenosky and Stanfield 1975, Schmitz and Kolenosky 1985, Schmitz and Lavigne 1987). Third, the eastern coyote has undergone a phenotypic response to enhanced food supply in the eastern range of coyotes (Thurber and Peterson 1991). Lastly, the eastern coyote is the result of hybridization between gray wolves (*C. lupus*) and expanding coyotes with subsequent selection for larger prey, specifically white-tailed deer (Silver and Silver 1969, Mengel 1971, Lawrence and Bossart 1975, Nowak 1978, Lariviere and Crete 1993).

We have found little evidence for coyote/dog inter-breeding resulting in hybrid coydog populations. Breeding experiments between coyotes and dogs (Silver and Silver 1969, Mengel 1971) revealed breeding asynchrony between the canid species and F1 hybrids, little or no parental care from coydog males, and deformities in several of the offspring. The authors concluded that viable coydog populations were not likely under natural conditions in the wild. Recent genetic evidence suggests that even wolves and dogs, which are the same species (*C. lupus*), do not readily inter-breed under natural conditions (Vila and Wayne 1998). An additional line of evidence discounting the viability of natural coydog populations is based on geography. The larger morphology of the coyote is observed in specific eastern regions of North America. However, one would predict that the ubiquitous presence of dogs throughout the US and Canada should result in similar hybridization elsewhere.

The second hypothesis (adaptation to larger prey size) and third hypothesis (phenotypic response to food supply) have generated some debate (Schmitz and Kolenosky 1985, Schmitz and Lavigne 1987, Thurber and Peterson 1991, Lariviere and Crete 1993). The debate stems from the role that genetic selection may have on the morphology of the eastern coyote and whether hybridization with wolves is necessary to explain the increased morphology of eastern coyotes. Laviviere and Crete (1993) identify a number of critical points in the approach taken by Thurber and Peterson (1991) in their suggestion that food supply, in the absence of genetic selection, can account for the size differential observed in the eastern coyote. One point of agreement in the debate is the need to apply genetic markers to confirm or refute the presence of wolf genetic material introgressed into the eastern coyote.

Considerable genetic evidence exists that wolves (identified as gray wolves at the time) in the Great Lakes and eastern regions of Canada have hybridized with coyotes (Lehman et al. 1991, Wayne and Lehman 1992, Roy et al. 1994). A major conclusion from these studies was that hybridization did not affect coyote populations (i.e., the introgression of genetic material through inter-breeding was unidirectional (coyote-to-gray wolf). These results do not support the introgression of gray wolf genetic material into coyote populations that expanded into southeastern Canada and the northeastern U.S. One possible reason that *C. lupus* wolf mtDNA has not been observed within eastern coyote populations (Lehman et al. 1991, Wayne and Lehman 1992) is the evidence of the North American history of eastern Canadian wolf compared with the gray wolf (*C. lupus*) (Wilson et al. 1999). The mtDNA of eastern wolves (*C. lycaon*) is related to coyote mtDNA and may have been misdiagnosed as originating from coyote and not from *C. lycaon*. An additional problem in the analysis of the populations included in the Roy et al. (1994) study that represent the range of the eastern coyote (southern Quebec and Maine) is that canid samples from these two regions were *a priori* classified as wolf or coyote based on morphology. This classification potentially biased the taxonomic designation of these canids in the interpretation of the genetic data.

We examined 8 microsatellite loci in eastern coyotes from New York the Frontenac Axis of southern Ontario and New Brunswick. The eastern coyote samples were compared to a population of eastern Canadian wolves from Algonquin Provincial Park, to a Texan coyote population, and to other North American canid populations (Roy et al. 1994). In an analysis of the genetic distance of eastern coyotes from New York (n=20) and New Brunswick (n=20) coyotes, the eastern coyote population grouped together and appear more distinct from other coyote populations that do not demonstrate hybridization with wolves (Fig. 1). The coyote populations from Minnesota and Maine contain samples from animals defined as coyote-like based on morphology with the more wolf-like animals from these regions classified as Minnesota and southern Quebec "hybridizing wolves," respectively (Roy et al. 1994).

We also applied an Individual-Index (I_I) that provides an individual-specific genetic score that describes an animal as originating from one of two populations or describes the animal as a hybrid between the two. An individual index (I_I) was calculated for each individual animal DNA profile using the following equation: $\Sigma \log (p_A/p_B)$, where p_A and p_B are the allele frequencies of a specific allele from population A and B, respectively. This LOD score value assesses the origin of the alleles in each animal based on a ratio of the frequencies from two populations. If there are similar allele frequencies in both populations, then the I_I values of individuals from both populations will follow a distribution around zero. An increasing positive score indicates an individual originated from population A, and a decreasing negative score indicates an individual originated from population B. In this application populations are representing canids from specific species.

I_I values for canids from New York, the Frontenac Axis, Ontario and New Brunswick were assessed using two database comparisons. The first two databases used in the analysis were Algonquin wolves versus Texas coyotes to assess whether the eastern coyotes represent pure *C. latrans*. Using these two databases, the eastern coyotes appear in the range predicted for hybrids and more wolf-like animals compared to Texas coyotes. The second analysis used the Algonquin wolves versus New York canids to assess at a finer scale whether individual canids demonstrated more wolf-like or coyote-like genetic profiles. Scatterplots of both database comparisons were generated (Fig. 2). New York (Fig. 2A) and New Brunswick (Fig. 2B) canids demonstrate I_I values in the range predicted for hybrids. The Frontenac Axis canids (Fig. 2C) revealed animals in the range of hybrid canids with a number of animals in the range observed for Algonquin wolves.these results support the introgression of eastern Canadian wolf genes into the expanding eastern coyote populations. This would not have been observed if wolf/coyote hybridization resulted in no introgression of wolf genetic material into coyote populations, as concluded in other genetic studies (Roy et al. 1994). Furthermore, the population structure of North American coyote populations was previously described as panmictic (Roy et al. 1994) with extensive gene flow throughout the continent. It is unlikely that population differentiation among coyote populations is sufficient to explain the differences observed between eastern and Texas coyotes using the I_I index. The above data support the fourth hypothesis listed. We conclude that eastern coyotes represent a hybrid between the eastern Canadian wolf (*C. lycaon*) and the coyote (*C. latrans*). Previous authors proposed the hybridization of coyotes specifically with *C. lycaon* (then described as *C. l. lycaon*) (Mengel 1971, Kolenosky 1971, Moore and Parker 1992). Despite the genetic evidence for hybridization, the introgression of wolf genes into eastern coyotes is not independent of selection acting on the eastern coyote hybrids based on prey size. In our opinion these hypotheses on natural selection acting on eastern coyotes are not mutually exclusive from wolf/coyote hybridization.

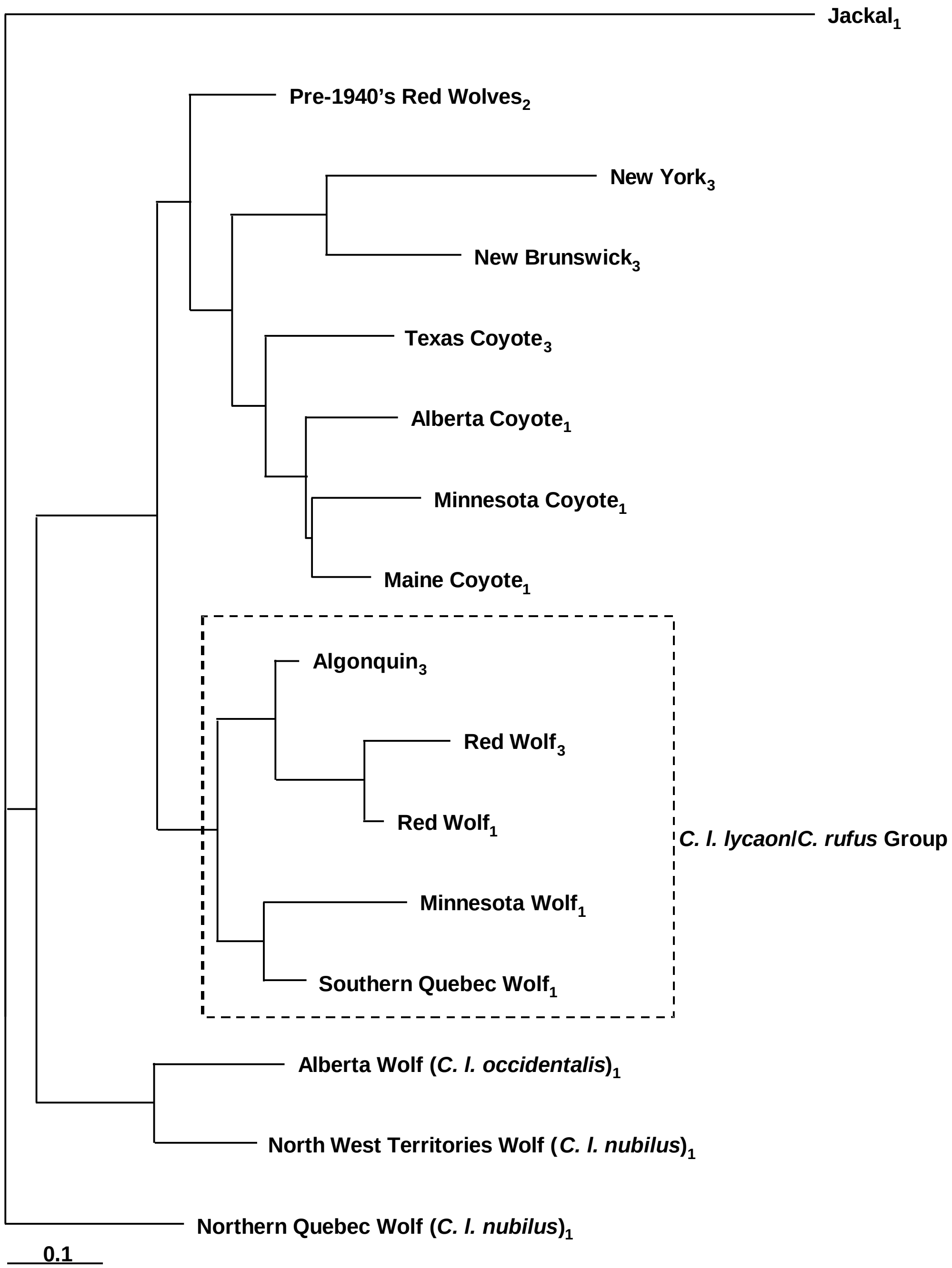


Figure 1. Neighbor-joining tree of Nei's unbiased genetic distances for allele frequencies from eight microsatellite loci. Number codes are provided to indicate the source of the allele frequencies from Roy et al. 1994 ($_1$), Roy et al. 1996 ($_2$) and this study ($_3$). Samples added in this study include: offspring from the red wolf breeding program (n=9); Algonquin Provincial Park (n=49); New York canids (n=20); New Brunswick canids (n=20); and Texas (n=20).

Fiure 2A. New York Canids

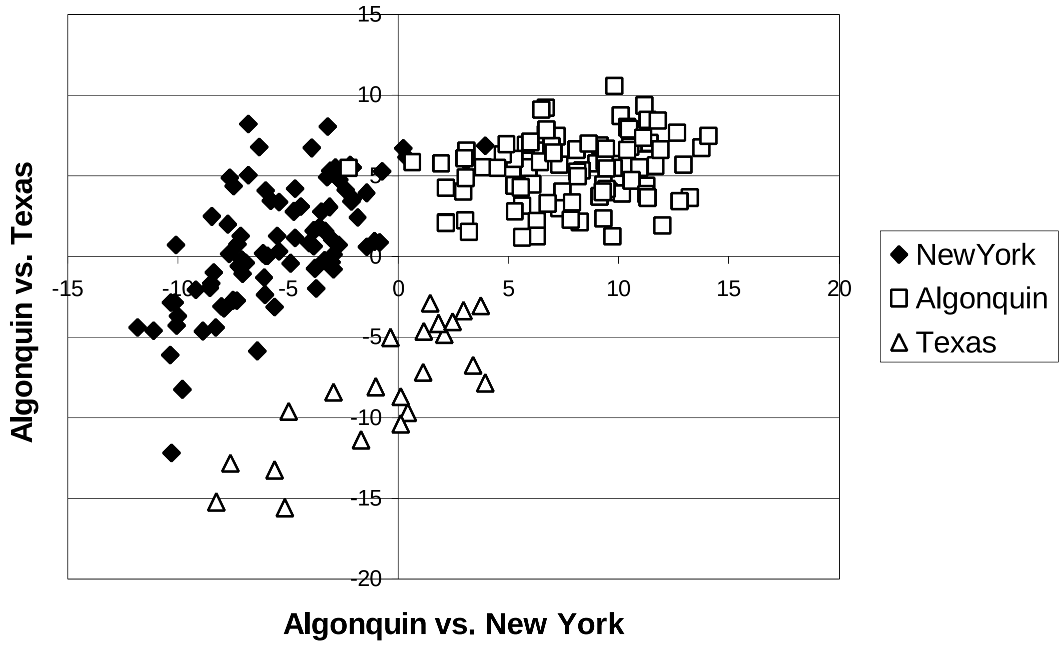
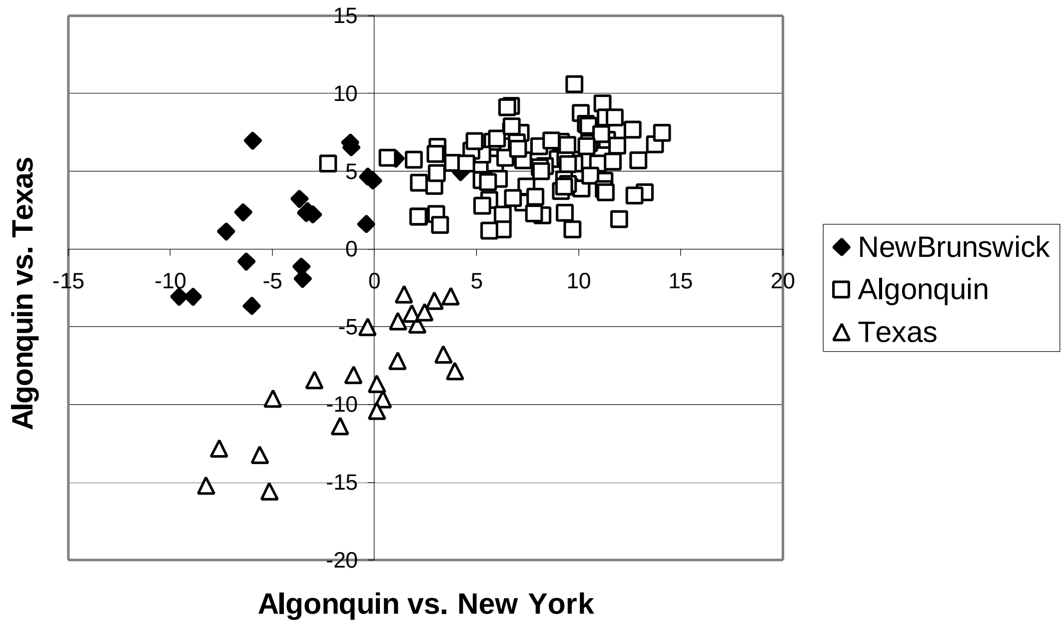


Figure 2B. New Brunswick Canids



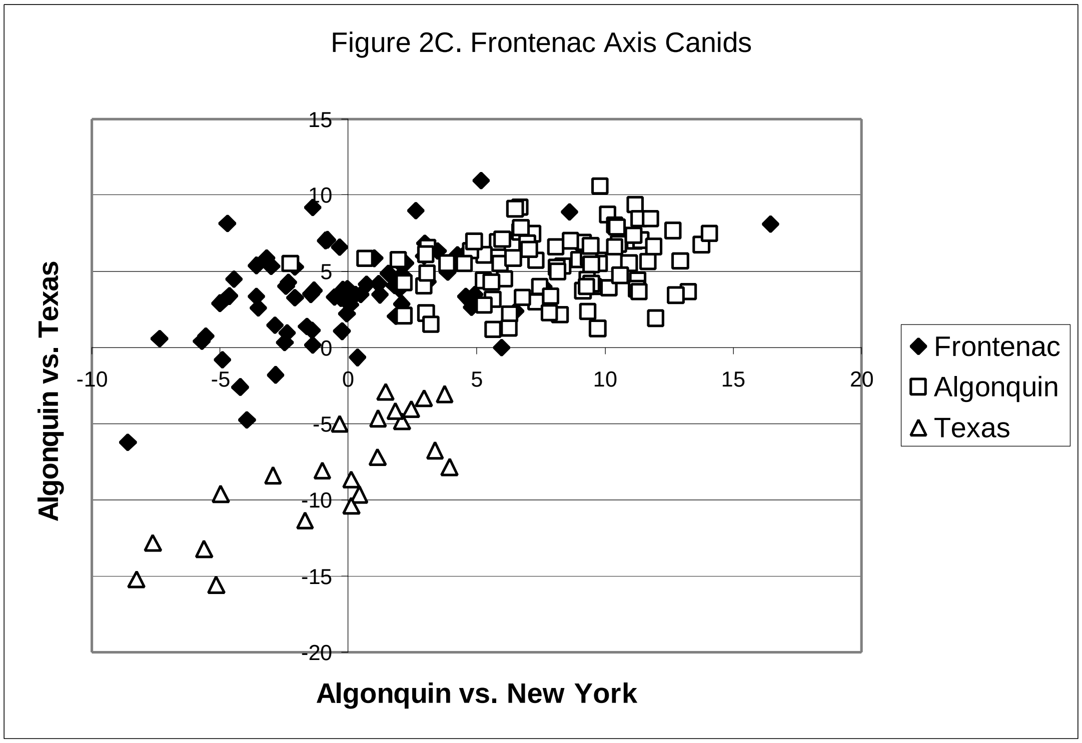


Figure 2. Log-likelihood individual indices (I_I) from eastern coyote canids, wolves from Algonquin Park and Texas coyotes. The I_I were calculated for each individual animal DNA profile at 8 microsatellite loci using the allele frequencies from the Algonquin Park/Texas coyote population and the Algonquin Park/New York populations. **A.** New York canids plotted on a scatterplot using the two comparisons. **B.** New Brunswick canids plotted on a scatterplot using the two comparisons. **C.** Frontenac Axis canids plotted on a scatterplot using the two comparisons.

MODELING WOLF HABITAT SUITABILITY

The recent development of spatially explicit theoretical models suggests that habitat selection by wolves is predictable at various spatial scales (Paquet et al. 1996, Alexander et al. 1996, and Mladenoff and Sickley 1998). Extensive fieldwork has verified the efficacy of these models (Appendix A). By generalizing site-specific empirical models, potential wolf habitat can be modeled in areas where wolves have been extirpated. However, important inputs for these models must be modified to reflect local conditions. Though modeling precisely how wolves might behave to a new environment is impossible (nature works under the laws of probability not absolutism), we can assess the feasibility of wolf reintroduction by building spatially explicit models based on field research.

Potential wolf habitat has been recently modeled for the northeastern US, including the Adirondack Park region, at a coarse spatial scale using only a few key criteria (Mladenoff and Sickley 1998). Using this modeling approach, favorable habitat conditions for wolves were identified in the Adirondack Park region (16,020 km ^{2}). The total area was considerably less than a previous estimate of 24,280 km ^{2} by the US Fish and Wildlife Service (1992).

In constructing a new habitat suitability model for the Adirondack Park, we derived model attributes from radiotelemetry and snow-tracking field data collected in the Rocky Mountains, Riding Mountain National Park (Manitoba), Pukaskwa National Park (Ontario), Minnesota, Wisconsin, and Italy. These areas differ significantly in landscape complexity, prey abundance, prey diversity, and extent of human development. The Adirondack Park, however, contains elements representative of all these areas. We supplemented these model attributes with habitat descriptors extracted from the relevant ecological literature. Where necessary, expert opinion was used to modify some model attributes. We also employed spatially explicit data sets at various scales (as fine as 1:24,000) and examined many additional aspects of wolf ecology not considered previously.

The Data

To conduct GIS-based (geographic information systems) analyses and models, spatially explicit digital (or computer readable) data must be assembled. With the help of many individuals throughout the Adirondack Park region, we were able to locate most of the datasets needed to construct reliable spatial models (see Table 1).

In GIS, data are usually discussed as a series of data layers (or themes). Layers are assembled as rasters (grid cells) or vectors (points, lines, and polygons). These layers are often referred to as the data "type." Resolution (the size of the smallest visible unit) is associated with raster data, and scale (relationship between distance on a map and distance on the ground) with vector data. For this study, some data layers were available only for the Adirondack Park (e.g., 1:24,000 roads), whereas other layers were available for the larger regional extent. Sources for the various data layers and timeliness of availability were varied. For the purposes of wolf habitat suitability and connectivity modeling, we also attempted to assess the quality of the data, which helps us evaluate the certainty of various modeled components. We used three GIS software packages: Arc/Info® and ArcView® by ESRI, and ERDAS Imagine® by ERDAS.

The goal of our study was to provide ecological information necessary to assess the potential of the Adirondack region to support gray wolves. The primary objective was to construct a series of spatially explicit gray wolf habitat suitability models. Output from the model identifies areas with high biological capacity to support wolves, most probably wolf travel routes, areas with low human presence, and sites where wolf-human conflict might occur.

We constructed this model by evaluating, and where possible integrating, the results of four submodels (core security area, den suitability, physical, prey base, and displacement). Because snow dramatically influences habitat use by wolves, we decided to model winter and summer seasons independently in some cases. Summer was defined as 15 April to 15 September and winter as 16 September to 14 April. These periods reflect important biological events that influence wolf movements (e.g., denning activity and pups travelling with adults as a pack). We also chose to model wolf habitat suitability under pristine conditions ("pristine" defined here as the absence of modern humans) in the AP. Though speculative, this retrospective view helps us understand how humans influence the distribution and viability of regional wolf populations. The basic spatial models created also provided the necessary information to produce a surface for simulating the movements of wolves in the AP and between the AP and the surrounding region.

The data layers used in the models were organized as physical, biological, and cultural factors. Figure 1 shows how the different data layers (shown as trapezoids) were used to generate the results for the summer season under current conditions. Note that shaded trapezoids represent data layers that resulted from additional analyses (e.g., the determination of slope from elevation data or the calculation of road density from a road layer). The winter model flowchart excluded den suitability, added snowfall as an important physical factor and snowmobile trails under the cultural heading. Whenever pristine conditions were examined, all of the cultural influences were omitted.

Core Security Area Submodel

As explained in the natural history section, in human dominated landscapes wolf survival largely depends on reducing contact with people. Therefore, we assessed the spatial distribution of human influences within Adirondack Park to identify areas of core security for wolves. We defined core security areas as sites where wolves are least exposed to humans and their activities. Lacking a human use layer, we evaluated all the cultural data layers as potential surrogates of human activities. We concluded the roads layer was the best proxy available for the analysis. Accordingly, we delineated l core security areas by buffering all 1:24,000 roads by 1km (see Plate 1). The 1-km buffer reflects the distance human activities are known to disturb wolves (Chapman 1977, Paquet et al. 1996, and the distance wolves try to maintain between humans and themselves (Singleton 1995 , Paquet et al. 1996).

After applying the buffer, 420 landscape polygons totalling 2,317,241 ha were identified. Polygons less than 15,000 ha were eliminated because we considered them too small to support a lack of gray wolves over time. We did not screen for polygon shape, distance between polygons, or condition of the matrix between polygons. Consequently, wolves may not have access to some sites because of impediments to movement. Therefore, wolves might not use some core areas identified as secure.

We identified eighteen core security areas that, depending on size, could function independently or collectively as linked habitat patches. The areas range in size from 15,051 ha to 202,998 ha. Land ownership (see Plate 2, Table 2) characterizes each site. We consider these sites the most secure areas for wolves within the AP. Note that our analysis accounts only for habitat security and not habitat quality. In most instances, wolves are attracted to high quality habitats and repulsed by human activities. In human dominated landscapes, these two factors interact to create a dynamic tension that wolves must balance to secure necessary life requisites. In some cases wolves are willing to sacrifice security for the benefits associated with high quality habitat. Conversely, wolves are easily displaced from poor quality habitats when exposed to low levels of human activities. All models were evaluated using these 18 core security areas as a landscape mask. In total, 1,100,775 ha (or 47%) of the AP is sufficiently secure to support wolves.

Table 2. Size and ownership composition of the 18 core security areas mapped for the Adirondack Park, NY.

Core Security #	Area (ha)	Area (ac)	Percent Private	Percent Easement	Percent Public
1	19,792	48,886	93.90	0.00	6.10
2	15,435	38,124	82.27	0.00	17.73
3	20,477	50,578	38.21	0.00	61.79
4	94,085	232,390	39.50	39.44	21.06
5	15,675	38,717	24.84	69.93	5.23
6	41,035	101,356	65.54	29.11	5.35
7	15,051	37,176	4.60	0.00	95.40
8	167,265	413,144	33.49	2.52	63.99
9	197,263	487,240	35.66	4.96	59.38
10	49,808	123,026	42.91	0.00	57.09
11	20,594	50,867	3.34	0.00	96.66
12	17,588	43,442	10.52	0.00	89.48
13	55,210	136,369	39.05	3.48	57.47
14	202,998	501,405	16.65	2.15	81.20
15	52,846	130,530	16.05	0.00	83.95
16	41,073	101,450	19.86	0.00	80.14
17	46,342	114,465	3.33	0.00	96.67
18	28,238	69,748	19.71	0.00	80.29
Totals	1,100,775	2,718,913	32.75	8.42	58.83

Physical Submodel

Although ecosystem generalists, wolves in mountainous regions concentrate activities in forested valley bottoms due to the effects of physiography, weather, prey distribution, and prey abundance (Paquet 1993, Paquet et al. 1996, Weaver 1994, Singleton 1995, and others). Wolves respond to movements of their prey, using valleys during winter, and increasing their range to more upland habitats during summer. Travel routes are usually composed of adjoining habitats or patches of habitat linked by natural linear features. Travel and habitat selection is influenced by availability of prey and location and connectivity of optimal inter-patch travel routes. Rugged topography severely limits the number of landscape linkages in mountainous areas by restricting movements. Although wolves are highly mobile, they cannot reach all areas of potential habitat if landscape connectivity is limited. Dispersal and immigration also are critical to the persistence of populations in marginal habitat. Data on characteristics of dispersal habitat are limited, but studies in the Rockies have identified topographic "funnels," prey patches, distance from centers of human development, and low human population density as factors favoring north-south dispersal along the Rockies from Banff to Montana (Boyd et al. 1995). Slope, aspect and elevation were finer-scale constraints on wolf movement within the Banff area and regions of Ontario (Paquet et al. 1997). In areas such as Ontario and Minnesota, where larger source populations are found in gentler terrain, effective dispersal occurs through semi-developed habitat (Mech et al. 1995, S. Fritts pers. comm.). Wolves have a preference for more gentle terrain and a tendency to prefer flat, west and southwest aspects during summer and winter months.

For the AP model, we created a map that reflects the suitability of the physical environment to support wolves. The initial physical model assumes no human activities have occurred. The probability that a species will use a certain area or travel a particular path is expressed as a function of known behavioral characteristics of wolves, the physical environment, and distribution of physical resources. For the summer season, we derived slope and aspect from the 1:250,000 DEM (Digital Elevation Model). We assigned wolf suitability scores and descriptions for slope and aspect based on radiotelemetry studies conducted in other regions. Table 3 provides suitability scores for the slope values and Table 4 provides the same for aspect. Slope and aspect suitability scores were then combined providing an overall physical use score (see Table 5).

Table 3. Slope wolf use probabilities, suitability descriptions, and scores.

Slope use probability	Suitability	Score
.5 – 6	Very low	1
6 – 11	Low	2
11 – 17	Moderate	3
17 – 22	High	4
22 – 28	Very high	5

Table 4. Aspect wolf use preferences, suitability descriptions, and scores.

Aspect in degrees	Suitability	Score
0 – 90	Poor	1
90 – 180	Fair	2
180 – 270	Good	3
270 – 360	Fair	4
-1 (flat)	Good	5

Table 5. Combined scoring of slope and aspect preferences to model probable wolf use in the Adirondack Park, NY.

Slope Score + Aspect Score	Suitability
2	Very low
3 – 4	Low
5 – 6	Moderate
7 – 8	High
9 – 10	Very high

Summer results for physical habitat suitability based on slope and aspect are provided in Plate 3. Note that the 18 core security areas are also shown. Relative amounts of each suitability class are distributed in the same proportions in the core security areas as with the entire AP (see Figure 2).

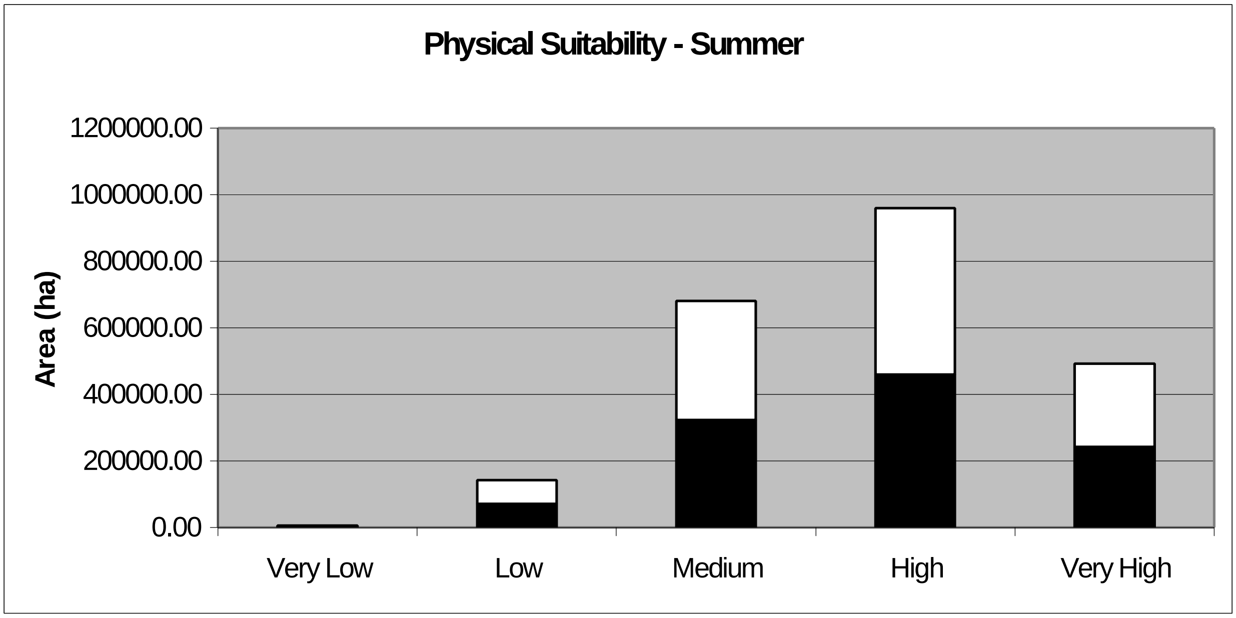


Figure 2. Physical wolf habitat suitability histogram for the entire Adirondack Park, NY for the summer. Black bars represent core security areas and white bars areas outside of core areas.

Given the relatively gentle terrain of the Adirondacks much of the area is physically suitable for wolf habitation. Topographic restrictions (e.g., steep slopes) prevent wolves from using only a small portion of the AP. When considering core security areas, approximately half the area of each histogram is not available to wolves.

Under winter conditions, snowfall impedance was introduced into the physical habitat model. Few studies have addressed the direct effects of snow on movements of wolves (Formozov 1946, Telfer and Kelsall 1984, Paquet et al. 1996). Fuller (1991) monitored wolf activity in north central Minnesota and found that wolves traveled farther and more often and spent less time with other pack members in mild than in severe winters. Wolves used conifer cover less when snow was shallow. The chest height of wolves is so low (approximately 40 cm) they have difficulty moving in snow deeper than 50 cm (Pulliainen 1982, Paquet et al. 1996).

We cannot accurately model the amount of precipitation that falls as snow over the various regions of the AP. Consequently, we assumed most November through March precipitation would fall as snow and estimated the degree of snow impact spatially. To approximate where snowfall would have its greatest influence on wolves in the AP, we scored mean monthly precipitation data (1961 – 1990) from the PRISM dataset for the months of November through March. Precipitation totals were mapped from this database using 3km x 3km grid cell sizes. Precipitation amounts were ranked 1 – 5 (1 = lowest precipitation; 5 = highest precipitation) for each month. To obtain a composite snowfall score, we totaled the ordinal (or ranked) scores for the five months. Final scores ranged from 5 – 25 and were assigned a final suitability description and score (see Table 6). This information was then factored into the existing slope-aspect model previously described by subtracting the snowfall score from the combined slope-aspect score. Before that was done, the combined slope-aspect scores ranging from 2 – 10 were reassigned values ranging from 1 – 5 according to the order shown in Table 7. This method heavily weights the impact of snowfall on wolf use and, because of the coarse nature of the precipitation data, over-generalizes precipitation patterns.

Table 6. Precipitation ranking using mean monthly precipitation data from 1961-1990 for November through March in the Adirondack Park, NY. Values under the “Score” heading were subtracted from the slope-aspect results from the summer model.

Total precipitation score	Suitability	Score
5 – 9	Very high	0
10 – 13	High	1
14 – 16	Moderate	2
17 – 20	Low	3
21 – 25	Very low	4

In comparison with the summer model, our winter model shows a very different distribution of habitat that is physically suitable for wolves. A much larger proportion of the AP area is undesirable during winter, particularly the High Peaks and greater West Canada Lakes regions (see Plate 4). The histogram for the various suitability classes also differs markedly between summer and winter.

During the winter months, the most suitable wolf habitat is concentrated in the northeastern quarter of the AP with moderately good conditions in the northwest quarter. If we eliminate areas with road densities >0.6 km/km ^{2} (see Plate 5), a value chosen from a number of empirical studies (see Displacement Model – Road Effects), a large portion of the best winter habitat becomes unsuitable. We used road density as a proxy for human activity instead of core security areas because wolf packs are more mobile in winter than summer as a result of denning. We believe wolves would prefer core security areas with favorable snow conditions during winter, but their increased mobility makes road density a better predictor of human disturbance.

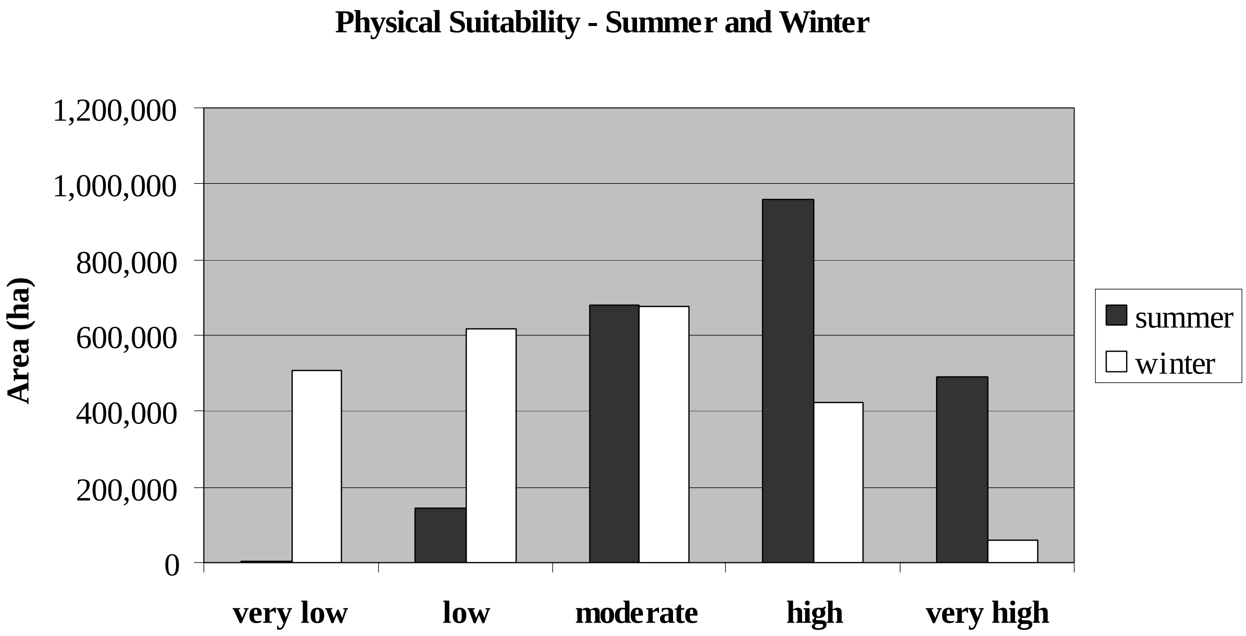


Figure 3. Physical wolf habitat suitability histogram for the entire Adirondack Park, NY for the summer and winter seasons.

Den Suitability Model

We modeled den suitability using two data layers (1:24,000 hydrology and 1:62,500 soils). Denning wolves prefer deep soils with adequate drainage near water. Denning wolves often prey on beaver (Carbyn 1983). Thus, availability of beaver may also influence selection of densites. In the AP as in other places, water is a reliable indicator of beaver. We modeled den suitability as follows:

1. Soil depth information was extracted from the soils database and assigned a suitability score (1 = poor; 5 = very good).
2. Soil drainage information was extracted from the soils database and assigned suitability scores (1 = poor; 5 = very good).
3. The 1:24,000 hydrology layer was buffered and suitability assigned to distance ranges according to Table 8.
4. Soils and hydrology scores were added providing a final suitability score (Table 8).

Table 7. Assigned den suitability based on distance from water for the Adirondack Park, NY.

Distance from water (m)	Den Suitability	Score
0 – 1	Unsuitable	No Data
1 – 100	Good	5
100 – 500	Fair	3
500 – 1,000	Poor	1
>1,000	Unsuitable	No Data

Table 8. Final den suitability scoring for the Adirondack Park, NY.

Hydrology + Soils	Den Suitability
No Data	Unsuitable
1 – 9	Poor
10 – 12	Fair
13 – 15	Good

The resulting map showing wolf den suitability is provided in Plate 6. The associated histogram for the entire AP under pristine conditions and within the mapped core security areas is provided in Figure 4.

Comparing den site suitability under pristine conditions versus core security areas showed a 52 percent loss of suitable den sites due to human displacement. A disproportionate amount of this loss (71%) came from the “good” category (see Table 9). What effect that would have on denning wolves is unknown, but the magnitude of the difference is noteworthy. Wolf denning habitat was found in all 18 core security areas. However, core areas in the northwestern quarter of the AP contained the largest contiguous denning sites.

Table 9. Comparison between pristine condition and present condition and den site suitability.

	Total Area (Pristine)	Core Security Area	Den Area Loss	Percent Loss
Poor	1360048.50	713231.50	646817.00	47.56%
Fair	497985.50	209417.00	288568.50	57.95%
Good	150237.25	43446.00	106791.25	71.08%
	2008271.25	966094.50	1042176.75	51.89%

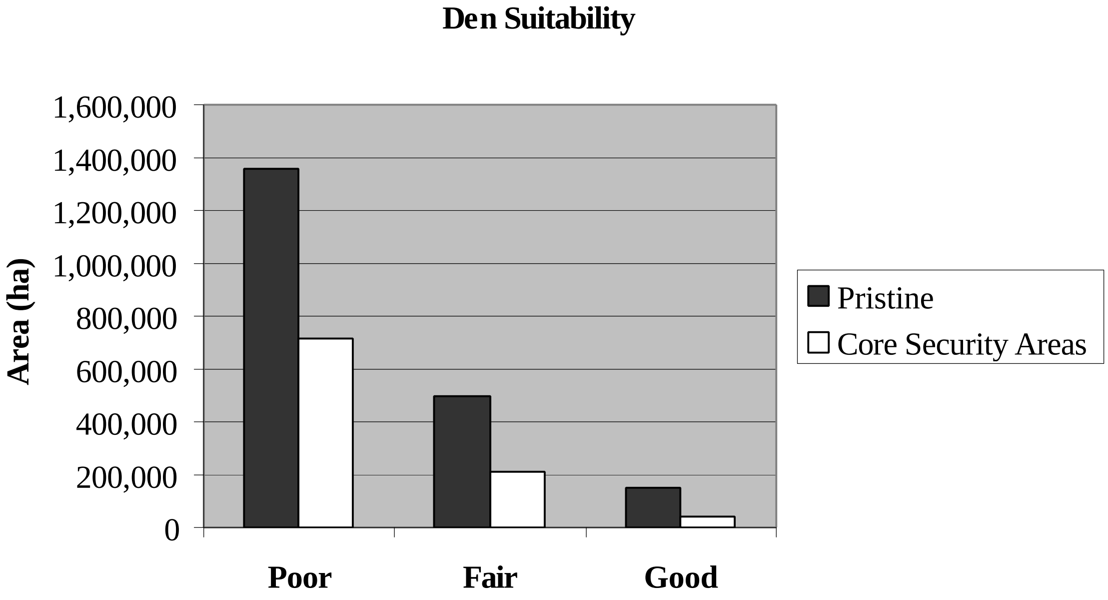


Figure 4. Den suitability for the Adirondack Park, NY under pristine conditions and for mapped core security areas.

Prey Base Submodel

Several studies suggest that a primary factor limiting wolves where they are present and tolerated by humans is adequate prey density (Fuller et al. 1992). Ungulates such as elk, deer, moose, and bighorn sheep make up most of a wolf's diet (Mech 1970, Fuller 1989), although they may eat smaller prey such as snowshoe hares and beaver. Ungulate biomass (Keith 1983, Fuller 1989), ungulate density, and ungulate species diversity (Boitani et al. 1997) have been significantly correlated with wolf density in some regions. For example, in a review of wolf demographics, prey density was shown to explain 72% of the variation in wolf density (Fuller 1989). A smaller core area, such as Riding Mountain NP (Manitoba), can support a viable wolf population if prey biomass per unit area is high (Fritts and Carbyn 1995). Ultimately, viable, well-distributed wolf populations are dependent on abundant and stable ungulate populations. Minimum deer density required to support a wolf pack is about 1 deer per square km (derived from Messier 1994). However, if given a choice, higher densities are sought out by wolf packs (Huggard 1991).

High prey biomass in biologically productive matrix lands could compensate for higher rates of human-caused mortality if connectivity is maintained with core areas (Fritts and Carbyn 1995, Haight et al. 1998). However, excessive mortality can cause these prey patches to become population sinks. For example, in areas such as the Banff/Jasper park complex, ungulates concentrate on winter range near human development, leading to high levels of mortality for wolves (Paquet et al . 1997). In the Greater Yellowstone Ecosystem, most ungulate winter range is outside of core protected areas, with seven of nine elk herds wintering outside the park (Fritts 1990, Fritts and Carbyn 1995). In Glacier National Park (US), the scarcity of ungulate winter range limits wolves to the western edge of the park (Fritts and Carbyn 1995). These wintering areas may function as "keystone" habitats if seasonal availability limits wolf population density (Fritts and Carbyn 1995). Similar "keystone habitats" may also exist in the AP.

We created a landscape surface that reflects the abundance and distribution of the current prey base within the AP. However, we consider this model weak because of the inherent difficulty in monitoring prey numbers and distribution. For example, we could not include moose data in the prey model because of sighting biases. In addition these points were not of the same quality as the deer density estimates. Deer density estimates were provided by the New York Department of Environmental Conservation (DEC). Density estimates were organized by township using a formula based on male deer killed by hunters in 1996. Some members of our advisory panel suggested that this technique under-estimates deer numbers, is organized at too coarse a level, is skewed by hunting effort, and does not consider recent landscape changes (e.g., 1998 winter storm damage and 1995 microburst damage) that could affect deer numbers. Based on the data acquired (including storm damage), we are much more confident in the spatial pattern of deer densities than population numbers.

Although deer would constitute the largest portion of a wolf's diet in the AP, beaver would be important during warmer seasons. Beaver become a significant prey item only when active. Wolves most frequently take them to feed young. Beaver density data are assembled by the New York Department of Environmental Conservation (DEC) according to wildlife management units. In the Adirondack region these units are quite large. The AP contains portions of three of these management units. Because beavers are intimately linked to water, we expressed their densities as number of colonies per km of river (or Lake Margin).

Our prey base model is based on the 1996 deer density estimates by township and number of beaver colonies per km from 1993 – 1994 management unit estimates. Plate 7 shows the deer density for the AP. Note that all classes represented have sufficient deer densities to support a pack of wolves except for the polygons colored dark red (0.5 – 0.9 deer per square km). Wolves would undoubtedly be attracted to the areas of high deer density. Also note, that most of the high-density areas in the eastern portion of the AP lack adequate security for wolves. Wolves attracted to these areas would likely be killed or displaced by human caused disturbances.

A map of the 1995 microburst and 1998 ice storm damage is provided in Plate 8. The large disturbed areas in north and northeastern AP are from the 1998 ice storm. The bands of damage in the western portion of the AP are from the microburst event in 1995. Most of the ice damage occurred outside of wolf core security areas resulting in little benefit to wolves. Therefore, the increased deer populations in these areas will not be readily accessible to wolves. The microburst damage, on the other hand, largely occurred within core security area #9 (the Five Ponds Wilderness region) and should result in higher deer densities over the next decade. The beaver density estimates reflect a similar pattern as the deer. That is, higher densities in the southeast and northwest portions of the AP (see Plate 9).

Summer wolf habitat suitability based on prey density was compiled using the following scores for deer densities (Table 10) and beaver densities (Table 11). Final results were scored according to the information provided in Table 12 and mapped (see Plate 10). Please note that only the high prey base areas in the northwestern corner of the AP are sufficiently secure for long-term wolf survival.

Table 10. Scoring of deer density for the Adirondack Park, NY.

Deer density per km ^{2}	Suitability	Score
0.5 – 0.9	Unsuitable	0
1.0 – 1.3	Low	1
1.4 – 1.8	Moderate	3
1.9 – 2.9	High	4
3.0 – 8.7	Very high	5

Table 11. Scoring of beaver density for the Adirondack Park, NY.

Colonies per km river	Suitability	Score
0.09	Low	1
0.16	Moderate	3
0.34 – 0.38	High	5

Table 12. Final scoring of wolf prey base for the Adirondack Park, NY.

Deer density + Beaver density score	Suitability
1 – 4	Low
5 – 7	Moderate
8 – 10	High

Plate 10 also shows prey densities at a relatively coarse resolution. The amount of each suitability class found in all the AP and in core security areas is provided in Figure 5. This figure differs from the den suitability figure, which describes the entire AP as pristine. In the former case, humans have little influence on the factors used in that model (i.e., hydrology and soils). Humans, however, profoundly influence prey populations. Before European settlement, beaver densities were probably higher in the southeastern section of the AP than today. Changes in deer density are less clear.

Nevertheless, we have a reasonable understanding about the distribution and abundance of prey in the AP. Populations of white-tailed deer and beaver appear more than adequate to sustain wolves. Moreover, recovering moose populations could augment an already substantial prey base. As might be expected distribution and abundance of prey varies considerably throughout the AP. Wolf populations would not likely reflect levels indicated by prey biomass because some prey populations occupy areas inhabited by humans and would thus not be available to wolves.

Overall, 44 percent of the AP shows low prey suitability, followed by 30 percent for moderate and 26 percent for high. Assuming wolves prefer core security areas, then we estimate a 36 percent loss in the low suitability area, a 78 percent loss in the moderate category, and a 54 percent loss in the high suitability class. For the core security areas considered collectively, 60 percent of the land area is classified as having low prey suitability, 14 percent moderate, and 26 percent high. All the sites classified as high are in the northwestern core areas (most or all of #5, #4, #6, #9, and #13).

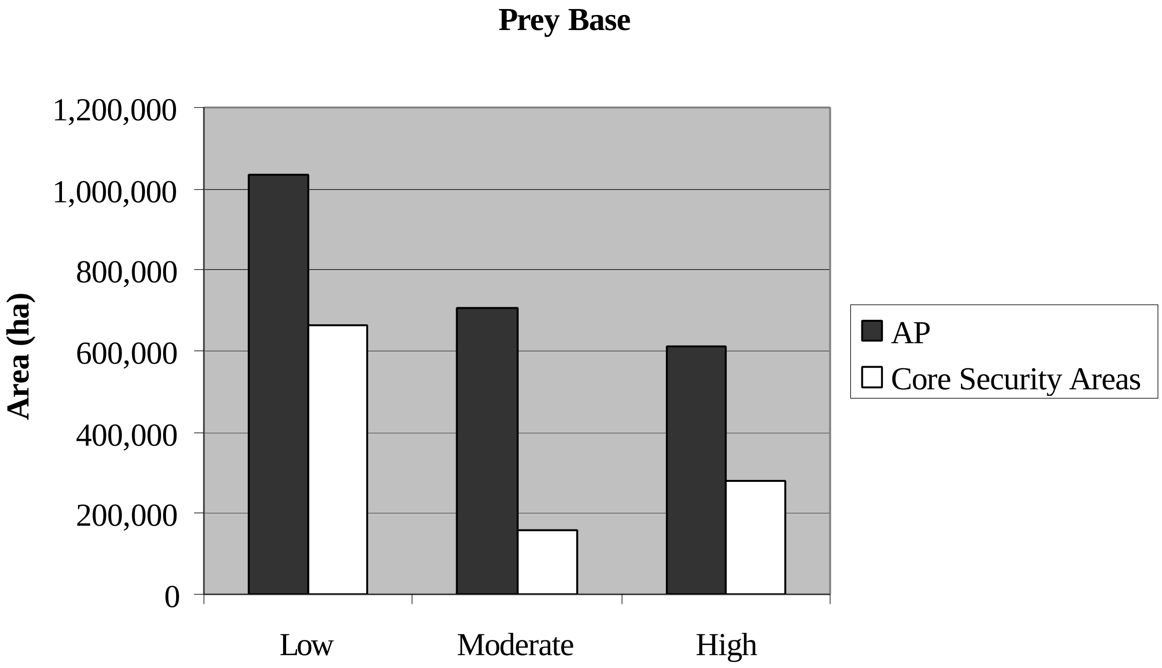


Figure 5. Prey base for all of the Adirondack Park, NY and for mapped core security areas.

Ranking Core Security Areas

We ranked core security areas based on the composite results of summer physical suitability, den suitability, and prey suitability. We did not consider winter physical conditions because wolf pack survival depends on the successful rearing of pups, which is a summer activity. However, wolves would be less attracted to some core security areas (even excluded) in harsh winter conditions. For example, based on the precipitation data, areas #14 and #18 would be unsuitable for wolves during winter, which lowers the overall value of these sites. That does not mean these areas could not, or would not, be used by wolves in the summer – these areas are just less suitable than other sites within the AP. Table 13 summarizes each core security area and how it scored for each criterion.

Table 13. Core security area ranking based on summer physical suitability, den suitability, and prey suitability for the Adirondack Park, NY.

Core Security Area	Physical Suitability Percent very high & high	Physical Suitability Ranking	Den Suitability Percent good & fair	Den Suitability Ranking	Prey Suitability Percent high	Prey Suitability Percent medium	Prey Suitability Ranking
1	64.8	3	38.0	4	0.0	99.7	4
2	61.4	3	26.6	3	0.0	99.8	4
3	68.8	3	24.4	3	44.3	55.5	4
4	75.9	4	33.0	4	99.9	0.0	5
5	72.1	4	29.1	3	99.8	0.0	5
6	81.4	5	45.2	5	99.9	0.0	5
7	42.0	1	22.0	3	0.0	53.4	3
8	47.8	1	17.0	2	4.3	4.7	1
9	73.0	4	26.4	3	30.6	18.4	4
10	55.8	2	17.1	2	0.0	0.0	1
11	47.2	1	16.4	2	0.0	5.3	1
12	50.7	2	20.0	3	0.0	99.8	4
13	87.0	5	32.3	4	95.2	0.0	5
14	65.4	3	19.0	2	0.2	0.4	1
15	49.1	1	15.4	2	0.0	0.0	1
16	50.5	2	19.2	2	0.1	53.7	3
17	50.3	2	9.5	1	0.0	11.1	2
18	79.1	4	21.0	3	0.0	40.3	3

We added the three rankings together to generate a composite score for each core security area. Results ranged from 4 – 15 and were partitioned into three classes – poor (4-5), fair (6-10), and good (11-15). Six of the eighteen areas were ranked as good, seven as fair and five as poor (see Plate 11). The biophysical and human elements that collectively determine habitat quality of core areas vary markedly throughout the AP. As a result, habitats likely to be occupied by wolves are often discontinuous with one another. This means wolves need to move between habitat patches to survive. The intervening matrix between these patches might not be hospitable to wolves, which could adversely affect survivorship. In summary:

1. We have more confidence in the location of prey densities than we do in the density values.
2. Core security areas are the likely places for successful wolf presence.
3. Not all core security areas score the same based on physical suitability, den suitability, and prey densities.
4. Without humans, wolves would likely prefer most of the areas where towns exist today.

Displacement Submodel

Road Effects

Roads, by increasing human access, have been documented to negatively affect wolf populations at local, landscape (Fuller 1989, Thurber et al. 1994, Paquet et al. 1997), and regional (Mladenoff et al. 1995, Boitani et al. 1997) scales. Roads may act as mortality sinks through highway deaths or by providing easier access for hunters and poachers. In severe cases, roads can cause population changes through mortalities, loss and alteration of habitat, and disturbing activities. Besides functioning as a source of direct mortality, roads also may be physical or psychological impediments to wolf movement. Although researchers have documented dispersal across major highways for wolves in Minnesota (Mech et al. 1995), Montana (D. Boyd pers. comm.), and Alberta (Boyd et al. 1996), some may function as partial barriers or filters (Paquet et al. 1997). Roads also may function as disturbance factors (Paquet and Callaghan 1996, Paquet et al. 1997). Road data can be incorporated into a model as distance from road, size of contiguous roadless area, or road density (using a variety of computer mapping techniques). The "distance from road" metric may be more appropriate at finer scales. An avoidance zone of 500 m was documented in Banff National Park (Paquet et al. 1996). Thurber et al. (1994) showed a negative response up to 5 km from roads in Alaska. In winter, wolves also are attracted to roads for ease of travel (Thurber et al. 1994, Paquet et al. 1996).

Human activities that compact or clear snow (e.g., snowmobiling, cross-country skiing, and maintenance of winter roads) may alter winter movements of wolves by providing economic travel routes into areas that are usually inaccessible because of deep snow. This may distort winter home ranges, affect the rate of wolf predation on ungulates (Okarma et al. 1995), and change the pattern of selection for species and cohorts (Paquet 1989). In areas where forest cover and human activities adjoin, travel routes that are efficient to follow may attract wolves to agricultural and urban areas (E. Pullianen, pers. commun.).

In human dominated landscapes, road density becomes the more relevant metric at landscape and regional scales (Mladenoff et al. 1995, Boitani et al. 1997). Studies in Wisconsin, Michigan, Ontario, and Minnesota have shown a strong relationship between road density and the absence of wolves (Thiel 1985, Jensen et al. 1986, Mech et al. 1988, Fuller 1989). Wolves generally are not present where the density of roads exceeds 0.58 km/ km^2 (Thiel 1985 and Jensen et al. 1986, cf. Fuller 1989). Landscape level analysis in Wisconsin, Minnesota, and Michigan found mean road density was much lower in pack territories (0.23 km/ km^2 in 80% use area) than in random nonpack areas (0.74) or the region overall (0.71). Road density was the strongest predictor of wolf habitat favorability out of five habitat characteristics and six indices of landscape complexity (Mladenoff et al. 1995). Few areas of use exceeded a road density of >0.45 km/ km^2 (Mladenoff et al. 1995). Notably, radio collared packs were not bisected by any major federal or state highway. In Minnesota, densities of roads for the primary range, peripheral range, and disjunct range of wolves were all below a threshold of 0.58 km/ km^2.

These results, however, probably do not apply to areas on which public access is restricted. Mech (1989), for example, reported wolves using an area with a road density of 0.76

km/km², but it was next to a large, roadless area. He speculated that individuals that dispersed from the adjacent roadless area compensated for excessive mortality experienced by wolves in the roaded area. Wolves on Prince of Wales Island, Alaska currently use areas with road densities greater than 0.58 km/ km². This may reflect the limited options wolves have to relocate when they live on islands or insularized landscapes. Road density thresholds in the more open landscapes of the Rockies may differ from those reported in the above studies (Weaver et al. 1996). Topographic effects also influence how road densities influence wolves. For example, in mountainous landscapes roads and usable wolf habitats converge in low elevation valley bottoms. Effective road densities calculated only for valley bottoms differ dramatically from densities calculated using the full areal extent of a wolf pack's home range.

There are several plausible explanations for the absence of wolves in densely roaded areas. Wolves may behaviorally avoid densely roaded areas depending on the type of use the road receives (Thurber et al. 1994). In other instances, their absence may be a direct result of mortality associated with roads (Van Ballenberhe et al. 1975, Berg and Kuehn 1982).

However, even in areas where nominal protection of wolves is high, 90% of mortality is human-caused (Pletscher et al. 1997). Despite legal protection, 80% of known wolf mortality in a Minnesota study was human-caused (30% shot, 12% snared, 11% hit by vehicles, 6% killed by government trappers, and 21% killed by humans in some undetermined manner) (Fuller 1989). Mech (1989) reported 60% of human-caused mortality in a roaded area (even after full protection), whereas human-caused mortality was absent in an adjoining region without roads. On the east side of the central Rockies between 1986 and 1993, human-caused mortality was 95% of known wolf death. Thirty-six percent (36%) of mortality was related to roads (Paquet 1993). Though offering only partial protection, parks such as Banff and Glacier have historically played a critical role as sources for recolonization (Boyd et al. 1995).

Wolves in Minnesota and Wisconsin are now occupying ranges formerly assumed to be marginal because of prohibitive road densities and high human populations (Mech 1993, Mech 1995, D. Shelly pers. comm.). Legal protection and changing human attitudes are cited as the critical factor in the wolf's ability to use areas that have not been wolf habitat for decades. Nonetheless, wolves in Minnesota continue to avoid populated areas, occurring most often where road density and human population are low (Fuller et al. 1992). Dispersers or marginalized individuals may be pushed into suboptimal habitat as dominant animals or packs saturate more suitable and safe habitat

Clearly, the influence of road density on wolves has been well documented, and the resulting spatial models from a number of studies have been proven to be very dependable. The AP contains approximately 8,195 km (5,092 miles) of roads. We modeled road density using the 1:24,000 roads data layer from the AP GIS. A 1-km x 1-km grid cell array was made for the entire AP and road density calculated for each cell. These results were then generalized using a moving window function 5 km x 5 km in size (see Plate 12). Class cut- offs were chosen based on empirical data from similar analyses from other parts of the United States and Canada. High suitability was mapped for road densities of 0-0.23 km/km ^{2}, medium for densities of 0.23-0.45 km/ km², and low for densities of 0.45-0.6 km/ km ^{2}. Areas with road densities >0.6 km/ km ^{2}

were considered unsuitable for wolf survival. Note the location of the core security areas and the relative wolf habitat suitability based on road density between areas. These areas become particularly important when modeling the likely inter-regional movement corridors.

Human Population Effects

Human activities have been shown to influence the distribution (Thiel 1985, Fuller et al.1992, Paquet 1993, Mladenoff et al.1995) and survival of wolves (Mech et al.1995, Mladenoff et al. 1995, Paquet 1993, Paquet et al. 1996). Although human-caused mortality is consistently cited as a major cause of displacement (Fuller et al. 1992, Mech and Goyal 1993, and others), we have limited empirical information on tolerance of wolves to indirect human disturbance. However, information is available on human population densities that displace wolves. We have incorporated these data into our model.

We are aware of only four studies that have systematically and explicitly examined human population density and wolf distribution. In all studies, the absence of wolves in human-dominated areas may have reflected high levels of human-caused mortality, displacement resulting from behavioral avoidance, or some combination of both. All were conducted at a landscape scale and assessed population or pack level responses of wolves to humans. In Wisconsin, human population density was much lower in pack territories than in nonpack areas. Wolf pack territories also had more public land, forested areas with at least some evergreens, and lower proportion of agricultural land. Overall, wolves selected those areas that were most remote from human influence (Mladenoff et al.1995) using areas with fewer than 1.54 humans/ km^2. Most wolves in Minnesota (88%) were in townships with <4 individuals/ km^2 or with <8 individuals/km^2. High human densities likely precluded the presence of wolf packs in several localities within contiguous, occupied wolf range (Fuller et al. 1992). However, road density, a highly correlated variable, may provide greater predictive power in a multivariate model (Mladenoff et al. 1995), especially in regions characterized by high levels of recreational hunting mediated by road access.

Boitani (1995) analyzed the record of human/wolf coexistence in southern Europe versus that of wolf extirpation in northern Europe. Human population density was only one of several factors determining the ability of the two species to coexist. A settled agricultural, rather than pastoral culture, lack of organized governmental eradication efforts, and high topographic heterogeneity contributed to the survival of wolves in southern Europe. In Italy, wolf absence was related to human density, road density, urban areas, cultivated areas, and cattle and pig density. However, because human density, road density, and urbanized areas were highly intercorrelated no specific human effect was established (Duprè et al. in press).

In the Bow River Valley, Alberta the selection or avoidance of particular habitat types was related to human use levels and habitat potential (Paquet et al. 1996). Wolves used disturbed habitats less than expected, which suggests the presence of humans altered their behavior. Very low intensity disturbance (<100 people/month) did not have a significant influence on wolves, nor did it seriously affect the ecological relationships between wolves and their prey. At low to intermediate levels of human activity (100-1,000 people/month), wolves were dislocated from suboptimal habitats. Higher levels of activity resulted in partial displacement but not complete abandonment of preferred habitats. As disturbance increased, wolves avoided using some most favorable habitats. In portions of the valley where high elk abundance was associated with high road and/or human population density, wolves were completely absent. Overall, habitat alienation resulted in altered predator/prey relationships.

The degree of human influence probably varies according to the environmental context. If a particular habitat is highly attractive, wolves appear willing to risk exposure to humans, at least within some limits (Chapman 1977). The presence of artificial food sources (e.g., carrion pits, garbage dumps) also attracts wolves and reduces avoidance of human activity (Chapman 1977, L. D. Mech pers. comm., Paquet 1996).

For our analysis, we depended on roads and land use to predict exclusion of wolves by humans and for creating a movement cost surface. We examined 1990 census data, but dropped it from the analysis for two reasons. First, the data are 10 years old. Second, human use of the AP varies widely from 130,000 permanent residents to seasonal visitation of over 10 million each year (Schneider 1997). The Census data did not adequately account for this human population dynamism.

Wolves do not necessarily avoid roads. For example, wolves in the central part of Eurasia moved seasonally from the mountains where snow was deep to valleys with little snow, preferred to use plowed roads (Formozov 1946, D. Bibikov pers. comm.). Zalozny (1980) found that road networks cleared of snow allowed wolves to travel farther and thereby increased access to prey over a larger area. In Sweden, wolves avoided high snowfall areas above 1,000 m and traveled primarily along valleys with roads and across plateaus (Bjarvell and Isakson 1982, A. Bjarvell pers. comm.). Roads are problematic because they are a direct cause of mortality via collisions with vehicles. Equally important, roads provide access for humans to wildlands and thus increase opportunities for direct persecution of wolves. In other words, it is the lethality of roads that influences survival of wolves.

Other Anthropogenic Influences

There are numerous anthropogenic influences in and around the AP. These influences were integrated to create a cost surface that was used to predict the most likely travel corridors for wolves within the AP. Plate 13 shows the cultural features that would affect wolves.

Snowmobile Trails

Snowmobile trails have mixed influences on wolves. Access provided by winter trails may lead to harassment or killing of wolves. Conversely, wolves travel more efficiently through areas with deep snow by using winter wildlife trails or other compacted travel routes such as snowmobile trails (Mech 1970). The total length of registered snowmobile trails in the AP is 2,381 km (1,479 miles). These trails are concentrated in several places. Among the core security areas, snowmobile trail density is highest in Core Area #6. That area also rated the highest habitat suitability of all 18 core areas evaluated in the composite model. Accordingly, the likelihood of winter encounters with wolves would be high in this region.

Railroads

With one possible exception, railroads pose minimal threat to wolves in the AP. The AP has four railroad spurs penetrating the region with 520 km (323 miles) of rail line leading to four terminal destinations – Ausable Forks, Newton Falls, Tahawus, and Lake Placid. The track leading to Ausable Falls enters the region from the southeast and hugs the Lake Champlain shoreline until it approaches Ausable Falls where it heads west. The entire length of this spur is in poor wolf habitat. The tracks leading to Tahawus enter the AP from the southeast and also stay largely in poor wolf habitat. Tracks leading to Newton Falls enter the AP from the west just above the Five Ponds area. The only length of track that could pose a serious threat to wolves is the one leading to Lake Placid. It enters the AP from the southwest, cuts between the Ha-De-Ron-Dah Wilderness and the Canada Lake Wilderness. As it travels north and then northeast, it bisects the core security area containing the Five Ponds Wilderness. The threat posed by railroads is associated with location and traffic frequency.

Land Use

In Plate 13, we classify land use into five categories of wolf suitability. The various land classifications provided by the AP GIS were recoded as low, medium, or high wolf suitability (see Table 14). In general, the lowest scores were assigned to developed areas inside the AP, medium scores for resource management lands, and high scores to most public lands. One fairly good size area was not classified. Using land use as the discriminator, 3.25% (76,579 ha, 189,227 ac) of the AP was classified as low wolf suitability, 49.52% (1,166,639 ha, 2,882,765 ac) as medium, and 40.89% (963,368 ha, 2,380,482 ac) as high. The remaining 6.34% (149,195 ha, 368,661 ac) is occupied by water and a small unclassified area.

Table 14. Land classifications from the AP GIS land use data layer and wolf suitability ranking for the Adirondack Park, NY.

Land Classification	Wolf Suitability
Canoe Area	High
Hamlet	Low
Historic	Low
Industrial Use	Low
Intensive Use	Low
Low Intensity Use	Medium
Moderate Intensity Use	Low
Pending Classification	Unclassified
Primitive	High
Resource Management	Medium
Rural Use	Medium
State Administrative	Low

Water	Water
Wild Forest	High

WOLF CONNECTIVITY MODELING

We used least-cost path analysis for examining landscape connectivity for wolves in the AP for summer and winter conditions. Different landscape elements, human activities, and physical structures variably inhibit movements of animals including wolves. Other features enhance movements by attracting different species (e.g., high prey densities for wolves) or allowing them to move more efficiently through the landscape (e.g., plowed winter roads, highway underpasses). Linear developments such as roads and railways function as potential barriers to movement. The extent to which a particular impediment blocks movement varies. Thus, the range in permeability depends on the type of linear development, physical location, and amount of associated human activity. (Appendix B summarizes briefly current thinking about movement corridors.) Specific attributes for all features are expressed within the model as landscape coefficients collectively assigned to individual pixels. The values combine to create a landscape surface with a variable resistance to the movement of wolves. Each value represents how easily a wolf can move through a 1-km x 1-km pixel. Table 15 summarizes the cost assignments based on land class, road density, water, towns, and slope. Total summer cost was calculated by adding the components together (summer cost surface = land class surface + road density surface + water surface + towns surface + slope surface). Table 16 includes those changes/additions to the winter cost surface. In the winter, ice replaced water, and two other factors were added including snowmobile trails and probable snowfall. The formula used to produce the winter cost surface was winter cost = land class surface + road density surface + towns surface + ice surface + snowmobile surface + snowfall surface + slope surface. Cost to wolves ranged from 0 (no cost) to 10 (high cost). Cells assigned as “no data” were cost prohibitive for use by wolves.

Table 15. Summer cost surface assignment for the Adirondack Park, NY.

Land Class Surface	**Cost**
Canoe Area	1
Hamlet	No Data
Historic	No Data
Industrial Use	No Data
Intensive Use	No Data
Low Intensity	5
Moderate Intensity	No Data
Pending Classification	0
Primitive	1
Resource Management	5
Rural Use	5
State Administrative	No Data
Water	No Data

Wild Forest	1
Road Density Surface (road density km/km ^{2})	**Cost**
0 – 0.23	0
0.23 - 0.45	5
0.45 – 0.6	10
>0.6	No Data
Towns	**Cost**
All towns buffered by 500m	No Data
Slope Surface (probability of slope use)	**Cost**
0.6 – 7.5	10
7.5 – 14.4	5
14.4 – 21.3	2
21.3 – 28.2	0

Table 16. Winter cost surface assignment for the Adirondack Park, NY.

Land Class Surface	**Cost**
Canoe Area	1
Hamlet	No Data
Historic	No Data
Industrial Use	No Data
Intensive Use	No Data
Low Intensity	5
Moderate Intensity	No Data
Pending Classification	0
Primitive	1
Resource Management	5
Rural Use	5
State Administrative	No Data
Water	2
Wild Forest	1
Road Density Surface (road density km/km ^{2})	**Cost**
0 – 0.23	0
0.23 - 0.45	5
0.45 – 0.6	10
>0.6	No Data
Towns	**Cost**
All towns buffered by 500m	No Data

Slope Surface (probability of slope use)	**Cost**
0.6 – 7.5	10
7.5 – 14.4	5
14.4 – 21.3	2
21.3 – 28.2	0
Snowmobile Trail Surface	Cost
Present	1
Absent	2
Snow Surface (total precipitation score)	**Cost**
5 – 9	2
10 – 13	4
14 – 16	6
17 – 20	8
21 – 25	10

To simulate wolf movement in the AP, we ran four iterations using the summer and winter cost surfaces. We selected the three largest core security areas and one in the northern section of the AP. Four departure points exiting the AP (north, south, east, and west) were identified and used as destination points from each of the core security area polygons. Least cost path travel route simulations were run. The results provide multiple possible routes with weighting on the least expensive avenue from a defined starting point to a defined destination point. Simulated wolf packs should select travel routes that provide an optimal combination of security, habitat quality, and energetic efficiency. Conversely, wolves would variably avoid human facilities and activities, terrain that is difficult to negotiate, and habitat of low quality. In reality, wolves could move in many different ways – some dispersing wolves would be killed, others would find their way through the landscape. The least-cost path analyses delineate the optimal pathways for travel as defined by the cost surface (or friction) layer. We assume wolves would preferentially use these pathways given. Other (more sophisticated) connectivity modeling techniques are available, but the least-cost path analysis is a good first approximation. Pathways identified are similar to those derived using more complicated procedures and reflect closely the movements of wolves (Paquet et al. 1996).

The results for the summer and winter simulations are provided in Plate 14 and Plate 15. Several general observations can be made about the model outcomes:

1. Movement patterns differ between summer and winter conditions.
2. Winter movement patterns are more direct.
3. During the summer, movement out of the AP to the east (as we have defined it) is not possible.

4. Movement during the winter (when it is more likely) is more costly for wolves than during the summer.

5. A large percentage of the land area within the AP is prohibitively costly to wolf movement.

We considered the question of connectivity from a regional perspective (between the AP and the surrounding region) by calculating road densities for the surrounding region. We used 1:100,000 U.S. Geological Survey roads and calculated road density based on a 5-km x 5-km grid cell size. Our results (Plate 16) show the AP is isolated from the nearest potential wolf habitat, which concurs with the findings by Mladenoff and Sickley (1998). Even using these coarse level roads data (1:24,000 scale data usually show twice as many roads), the probability of wolves surviving very far into the matrix lands surrounding the AP is very low. This conclusion leads to the important issue of population viability in the AP if wolves were reestablished.

CONCLUSIONS AND RECOMMENDATIONS

Providing minimally roaded "core areas," keeping legal harvest within sustainable limits, and providing adequate habitat for an abundant, stable ungulate population, are all-important components of an effective wolf reintroduction and conservation strategy. We believe the goal of a reintroduction program is to establish wolf packs and not individual wolves. This is because packs are the essential social and biological units necessary for long term survival of wolf populations. From the literature and our own studies, we have identified the following essential ecological requirements necessary to sustain a breeding population of wolves within the Adirondack region:

- **The ultimate factor determining population viability for wolves is human attitude**. Regional planning can facilitate human/wolf coexistence by identifying spatial refugia or core areas with a level of protection sufficient to buffer populations against conflicts with humans. It also can identify optimal locations of buffer zones and corridors that will expand the effective size of core areas by allowing use of semi-developed lands while reducing the probability of human-caused mortality. Potential zones of human-wolf conflict often are in areas of highly productive habitat that have above-average human use, are spatial buffers between large core habitat areas and zones of high human use, or are likely to experience increased human influence in the future based on land-use and population trends. The interaction between food resource availability, carnivore movement patterns, and consequent mortality risks implies that the requirements for viability are location-specific, needing spatially-explicit analysis and an integrated approach to viability modeling that incorporates habitat requirements across multiple scales. Whether humans in the AP are tolerant of wolves or not is the focus of the companion social assessment. Based on other wolf reintroductions (e.g., Mexican wolf in the southwestern U.S.), a relatively few individuals can cause a reintroduction effort to fail.

- **Wolves require an adequate and accessible prey base**. At a minimum, wolves require a prey biomass equivalent to about 100-kg prey/ km^2. Adult prey species equivalents are approximately 0.25 moose/ km², or 1.0 deer/km². In multi-prey systems, which the Adirondacks are becoming, different prey may combine to provide the total biomass necessary to sustain wolves. Importantly, prey also must be available to wolves. For example, in Banff National Park, prey biomass east of the Town of Banff is adequate to sustain wolves, but the town and highway block access to the area. Mladenoff and Sickley (1998) reported similar distributions of wolves and white-tailed deer in Minnesota and Wisconsin. Our assessment suggests that prey numbers in the AP are sufficient to sustain wolves, though some prey associated with human development may not be available.

- **Wolf packs require well distributed patches of secure and high-quality habitat exposed to fewer than 1,000 people or events/month**. We have identified these potential core areas using our habitat models and road densities. The latter was used as a substitute for human activity because we lacked site specific information. Our results suggest the Adirondacks comprises adequate secure core areas and other high-quality habitats to maintain a small population of wolves. However, this assumes wolves will have access to these secure, quality habitats. The insular nature of the core areas can reduce the usefulness for wolves as shape, size, and distance between patches influences habitat quality. Nevertheless, the sum of partially connected habitat patches combined with larger contiguous habitats should provide wolves adequate security from humans and the life requisites necessary to sustain them.

- **Wolf packs must have opportunities to move safely among high-quality habitats contained within their home ranges**. This means protecting the network of trails that link these habitats. Thresholds for disturbance within travel linkages are not yet known, though standards can be temporarily inferred from habitat displacement values used in this report. Our models show the AP is highly fragmented. As a result, the spatial arrangement of secure habitats may preclude use of some areas by wolves because human activities and developments could impede access.

- **In human-dominated landscapes, regional subpopulations of wolves need to interact via dispersal or long distance forays**. Intra- and inter-refuge travel corridors reduce the possibility of local extinction and potential genetic isolation. Therefore, regions and habitats (interconnected) must be linked to allow for exchange and long-distance dispersal. Ensured connectivity also is important because wolves face a high risk of mortality from humans or vehicles when travelling across settled landscapes. This means regional corridors that provide linkages among subpopulations must be secure. We believe corridors connecting high-quality habitats within the Adirondacks are reasonably secure to ensure wolf packs can move about freely. However, linkages between the AP and other areas are tenuous. We doubt these linkages can be relied upon to maintain wolves over time. The extended distance between the AP and other populations of gray wolves amplifies the insecurity of these linkages.

- **Undisturbed and secure denning and rendezvous sites are necessary to sustain a population of wolves**. If wolves are reintroduced to the AP, known denning and rendezvous sites would need to be seasonally protected following confirmation of denning (i.e., buffered by 1.6 km (1 mi) restricted entry zones from 15 April through 30 July). We identified adequate denning areas for wolves living within the AP. Seasonal protection of these sites should not be a problem.

- **Annual sustained mean mortality for a population of wolves should be less than 30% of adult mortality**. Wolves can likely sustain higher mortality for short periods (e.g., 1-2 years). Mortality includes natural deaths and deaths by hunting, trapping, highway collisions, and railway collisions. We believe annual mortality would be high within the AP, possibly exceeding 30%. Combined with other causes of mortality, road and management related deaths could significantly affect population persistence, particularly during establishment phases of reintroduction. Before wolves occupy and secure home ranges, travel patterns will be exaggerated. Thus, exposure to roads and other causes of mortality will be increased. Highway mortality was the major cause of low survival for reintroduced lynx in New York State (Brocke et al. 1991). Clearly, this is an important lesson not to be ignored. If a reintroduction of gray wolves proceeds in the AP, we believe the initial population will need to be augmented annually to help offset mortality.

- **Within the primary home range of a wolf pack, permanent human densities should be < 0.4 people/km^2.** Again, using road densities as a proxy, we identified areas in the AP that meet this criterion. However, access to these areas is not assured because of impediments to wolf movements. In addition, human densities increase outside the AP, which limits the potential regional distribution of wolves. In the short term, this may benefit wolves by restricting them to non-agricultural areas where conflicts with humans are less likely. Yet, from a population perspective, reduced geographical distribution and fewer packs threaten persistence. We believe that over time, the adverse affects will outweigh the benefits.

- **Wolf packs require a road density < 0.27 km/ km^2 within core use areas**. Road density is calculated after removing areas that wolves are physically restricted from using. For example, wolves do not often use slopes more than 45°. In winter wolves avoid areas where they sink more than 45 cm in the snow. Road densities in most secure core areas identified for the AP are below the threshold. Assuming the presence of suitable habitat, we are confident wolves would use these areas. Notably, few areas of this type exist outside the AP. As elaborated above, the contrast between the AP and the regional landscape does not favor persistence of wolves.

- **In areas outside protected landscapes, access provided by roads increases exposure of wolves to people with guns**. Thus, the potential "lethality" of a road network modifies the density of roads that affects wolf survival. Where killing wolves is allowed, the density of traversable roads should be less than 0.6 km/ km^2 within the entire home range of a wolf pack. Again, regional road density is substantially higher than in the AP.

- **Where wolves are protected, the density of paved roads and railways should be less than 1.2 km/km^2 within the entire home range**. Within the AP, wolf packs would be able to establish home ranges that meet this criterion.

- **Traffic volume on highways accessible by wolves should be below 2,000 vehicles/day, which allows wolves to move across the roads**. Mortality increases rapidly as vehicles/day approach 4,000. We have not calculated traffic volumes for the AP or the region.

- **Speed limits on roads and railroads accessible to wolves should be less than 70 km/hr**. Currently, speed limits on many roads and railroads exceed this threshold. If wolves are re-established in the AP, critical crossing sites will need to be identified and speed limits adjusted. Several such 'speed zones' are already in place as crossings for white-tailed deer, which may coincide with the needs of wolves. Based on experience elsewhere, we are concerned about the adverse effects of road-related mortalities and injuries, especially during reestablishment when population numbers are low.

- **Ideally, major highways that exceed traffic volumes and speed limits should be elevated or buried where important wolf habitat or travel linkages are traversed**. Other less expensive, and less effective, types of passageways include underpasses and overpasses. All wildlife would benefit from these mitigations.

- **Diseases introduced by domestic animals are a potential threat to the viability of wolf populations**. This is a particularly difficult issue to address regionally. Generally, owners of domestic animals assure their animals are disease-free. However, new diseases can infect wild populations before being controlled domestically. The spread of Parvovirus into wild wolves in North America is a recent example of this occuring. Protection from possible exotic wildlife diseases (e.g., viruses of genus *Morbillivirus*) also needs to be considered.

Based on the above assessment, we do not believe gray wolves can be permanently reestablished in the AP. Though our analyses suggest that the AP comprises sufficient habitat to support a small population of gray wolves, regional conditions are not conducive to sustaining wolves over the long term (e.g., 100 years). Given current trends in regional development, we anticipate environmental conditions necessary to maintain wolves will deteriorate over the next 100 years. Most development occurs in areas preferred by wolves, and human activities will unavoidably increase the risk of death and injury for wolves. Increased development will decrease opportunities for wolves to move freely about, displace or alienate wolves from preferred ranges, and interrupt normal periods of activity — all detrimental to long-term wolf survival.

Indirect human influences can affect a wolf pack's chance to survive and reproduce. As wolves approach their limits of tolerance, they become increasingly susceptible to what would otherwise be minor influences. In the AP, natural landforms and the condensed arrangement of potential habitats in some areas may make wolves highly susceptible to the adverse effects of human disturbance. In less physiographically complex environments, such as the Great Lakes region, multiple travel routes link blocks of wolf habitat. Destruction or degradation of one or two routes usually is not critical because safe alternative routes are available. In contrast, wolves living in the AP may not be able to avoid valley bottoms or use other travel routes without affecting their fitness. Therefore, tolerance of disturbance may be lower than in other human-dominated environments (e.g., Minnesota, Wisconsin) where wolves can avoid disturbed sites without seriously jeopardizing their own survival.

Lacking an unambiguous commitment by governments to protect wolves in and outside the Adirondack Park, we doubt a reintroduction of gray wolves could be successful. The support by conservation biologists for large reserves—especially when they are isolated from other areas with similar habitat—stems from considerations of population viability for species with large home ranges and/or low population densities (e.g., gray wolves). Typically, a larger block of suitable habitat will contain a larger population of a particular species. All else being equal, large populations are less vulnerable than small populations to extinction as a result of deterministic or stochastic factors. In the AP, regional isolation would expose reintroduced gray wolves to the perils that threaten survival of all small populations. Lacking a source population of gray wolves to augment the local population, wolves in the AP would be subject to genetic problems that depress reproduction and accelerate mortality. More importantly, a small and isolated population of wolves would not be buffered against random catastrophic events such as disease, thus increasing the probability of extinction.

As described above, ecological conditions in the AP dictate against a successful reintroduction of gray wolves. A small population might exist for, say 50 years. However, we should not confuse existence with persistence. The latter implies perpetuity, which we believe is the unstated objective of most reintroductions. Even if conditions were correct for establishment of wolves, the issue of which canid species originally occupied the AP is unresolved. Recent evidence strongly suggests red wolves were endemic and the current dominant canid is a coyote hybrid. We believe that if gray wolves were never present, or existed only in low numbers, or as occasional visitors, then introduction of the species would be inappropriate. From an ecological perspective, the functional niche of a summit predator may be more important than which species fills the role. At present, that trophic position is putatively occupied by a hybrid canid.

The identification of coyote hybrids within New York State has important implications for the potential reintroduction of gray wolves into the Adirondacks. It is unknown whether expanding coyotes inter-bred with remnant wolves within New York that resulted in the large coyote hybrids or whether hybridization between eastern Canadian wolves and coyotes in Ontario was followed by the southern migration of hybrids into New York. Despite these two possibilities, historical accounts and genetic data from historic samples suggest the eastern Canadian wolf/red wolf (*C. lycaon*) was common within the State before extirpation. However, according to the 1800s account of De Kay (1842), wolves of gray wolf (*C. lupus*) origin may have been present, although rare. The recommendation for any relocation of wolves into the Adirondacks based on the genetic data would be to reintroduce the eastern Canadian wolf (*C. lycaon*). This assumes that relocation is feasible.

At present, the coyote hybrids inhabiting New York State are functioning as apex predators with a predominantly white-tailed deer diet. Specific questions should be addressed as to the additional role the eastern Canadian wolf would add to the Adirondack ecosystem. A comparison of the ecological differences between eastern Canadian wolves and eastern coyotes should be undertaken to determine what differences exist between the two predators. If the re-introduction of eastern Canadian wolves is intrinsically important because the species existed in New York State and was extirpated as a result of human activities, then the feasibility of maintaining a population of *C. lycaon* must be addressed.

Whether the relocation of eastern Canadian wolves into the Adirondacks will result in cohesive pack structures that will prevent inter-breeding with neighboring hybrid coyotes is unknown. Ongoing research programs on an eastern Canadian wolf population in Algonquin Provincial Park and a red wolf reintroduction program may provide insights. A genetic analysis of Algonquin wolves and neighboring Frontenac Axis canids has shown limited gene flow between the park and nearby canids (Grewal et al. in prep.). Conversely, the red wolf re-introduction program at Alligator River, North Carolina has confirmed hybridization between released red wolves and coyotes migrating into the area (Red Wolf PVHA). Moreover, this hybridization is occurring at low coyote densities. A comparison of these two systems is important to properly assess the effectiveness of maintaining the eastern Canadian wolf within the Adirondacks. We strongly recommended an initial study examine the variables influencing hybridization between *C. lycaon* and *C. latrans* before implementing a relocation program. The U.S. Fish & Wildlife Service red wolf reintroduction program has documented the effects of hybridization on reintroduced eastern wolves. The program has identified hybridization as its highest priority and is undertaking intense management actions to reduce the influence of hybridization.

If conditions are not right for the reintroduction of wolves today, what would it take to return wolves sometime in the future?

We agree with representatives of state agencies that a structured, well-organized, regionally integrated, and ongoing management plan is needed if wolves are ever introduced to the AP. Without such a plan, the long-term protection of biological assets necessary to sustain wolves is impossible.

The following section outlines considerations for development of a biologically defensible conservation strategy for wolves. The overarching theme is to sustain the natural environment and meet human needs by reducing the potential for one seriously to encroach upon the other. We hope our observations are viewed as a contribution to a comprehensive conservation plan for wolves and associated prey. Such a plan also might capture the needs of many other species. In formulating these comments, we tried to distinguish between information having some quantitative basis and that originating from subjective appraisals and intuition. Our comments are not intended to supercede or second-guess those individuals, organizations, and agencies who have given the subject of wolf reintroduction into the AP considerable thought. Following, in point form, are general observations regarding the establishment of wolves in the AP:

- Conservation efforts for wolf recovery should reflect biological/ecological time frames rather than social/political ones.

- Because wolves have such large spatial habitat requirements, management across regions and disjunct areas of suitable habitat is necessary. Therefore, conservation plans must address community, ecosystem, and landscape level issues . This requires cooperation among multiple government jurisdictions and private landowners.

- Unified regional management requires a broad systems approach that transcends the boundaries of Adirondack Park. To be effective, a wolf conservation strategy must consider the status of the entire regional metapopulation over an area that encompasses both source and sink populations.

- An essential first step is interagency cooperation based on a specific set of shared goals (e.g., ensure viability of all native species). This will require coordinating resource management and research with government with agencies and private interests managing adjacent lands.

- Biological science must be at the heart of any strategy to conserve carnivores, but social science, economics, law, education, and many other disciplines must be involved while finding politically acceptable solutions. The proximal threats to wolf recovery are related to habitat, but the ultimate threats are human population, behaviors, and attitudes.

- An outstanding challenge is the need to understand if and how we can preserve wolves within lands of multiple uses, including intense human activity.

- Recognizing that ideas about ecosystem management are still in a state of flux, future options should not be foreclosed by planning decisions that result in permanent removal of habitat .

- Although management should be based upon the best information available, unrecognized changes or events may occur. For example, population dynamics always contain an important (sometimes dominating) random component. Thus, predicting the future status of a regional population can be virtually impossible. Or, the discovery of a new rare species might require maintenance of a specific habitat to prevent extinction of the species. This unanticipated event could result in conflicts with other established management objectives. Accordingly, a fundamental principle of ecosystem management is that management should be adaptive, learning from experience, and changing in response to new ideas, information, and conditions.

- Many ecologists believe that some form of temporal and/or spatial refugia is prudent and perhaps necessary for persistence of wolf populations. The role of refugia in population persistence has emerged as one of the most robust concepts of modern ecology. Much remains to be known, however, about the actual size, dispersion, and spatio-temporal dynamics for effective refugia. We need further to assess the role of Adirondack Park as a potential core reserve for the region. Emphasis needs to be placed on identifying landscape connections with other nearby reserves.

- Ideally, conservation efforts should focus on the viability of the terrestrial carnivore guild, of which the gray wolf is a part. We suggest that a community approach to management, rather than single species management, is necessary to ensure persistence of all native carnivores and associated prey species.

- Develop a wolf conservation strategy (within the context of other species) based on empirical evidence of habitat requirements and tolerance of human activities to ensure that future development is compatible with the ecological requirements of wolves.

- Protect habitat quality in areas where there is potential for wolf populations to exist (i.e., "hold the line against additional degradation").

- Preserve linkages among potential subpopulations of wolves by protecting probable movement and dispersal corridors.

- Expand the width of "pinch points" along potential travel linkages to maintain the free flow of movement. Specifically, reduce human activities in and near constrictions and remove facilities that block or constrain movements along preferred routes.

- Provide for secure latitudinal and elevational movements in response to seasonal and long-term climate change. Winter travel routes often differ from summer pathways because of snow accumulation and effects of human activities. Managers need to consider the dispersion of humans on the landscape and types of activities being pursued.

- Restore impaired areas that wolves could use but that are marginally suitable because of disturbance. This may require managing human activities at different spatial and temporal scales (e.g., regionally, locally, seasonally, and daily). For example, managers can control the type and season of public use to reduce conflicts with wolves. Where necessary, alter patterns of human use by moving trails or facilities away from areas important for wolves (and other species).

- Specific management actions necessary to sustain wolves include increasing ungulate habitat capability, minimizing fragmentation of winter ungulate range, controlling potential sources of direct mortality on wolves, and providing additional unroaded or minimally roaded refugia for wolves. Significant progress toward these objectives is necessary to assure the viability and regional distribution of wolves.

- Managers need to assess critically the effects of human activities that modify natural snow cover. Non-essential roads and trails should not be maintained during periods of snow cover. In addition, activities that compact snow (e.g., snowmachines, dog sleds, snow shoeing, skiing) must be considered in relation to the distribution of prey, highways, towns, and other landscape features.

- Consider the need for habitat manipulation to mimic natural processes such as fire. Fire may be critical for sustaining a variety of successional habitats that support ungulates used by wolves.

- Highway and railway related mortality could be a threat to wolf survival in the Adirondack region. Anticipating future expansion of the regional road network, decision-makers should consider elevating and burying extensive sections of highways that pass through critical wolf habitat and travel corridors. In mountain landscapes, fencing, underpasses, and overpasses used to mitigate adverse highway effects have failed to provide adequate protection for wolves. However, in more homogenous landscapes (e.g., Great Lakes region), highway mortality has presented fewer problems. The Adirondack region is intermediate between western mountains and the Great Lakes.

- If trains are deemed a problem, we recommend that the speed of trains be reduced to 70 km/hr. During periods of heavy snow accumulation, speeds should be further reduced and trains should be preceded by ‘rail scooters’ to clear the track of wildlife. If suggested railway mitigations fail, then tracks should be strategically elevated for distances of at least 100 m to permit passage of wildlife underneath.

APPENDIX A

Modeling Approaches and Basic Literature Background

Several modeling methods have been used to analyze species/habitat relationships in wolves. A static predictive model of potential wolf distribution in the north-central U.S. used multiple logistic regression to analyze correlations between pack distribution and such landscape-level attributes as road density and fractal dimension (Mladenoff et al. 1995, 1997). The analysis scale, a moving window of 150 km ^{2}, was based on mean pack territory size. Boitani et al. (1997) used a similar approach to predict the potential distribution of wolves in Italy. They conducted discriminant function analysis (DFA), using a Mahalanobis distance metric, with a moving window of 100 km ^{2} (the mean pack territory size in Italy). The significant variables included: number of ungulate species, landscape diversity, human population density, road density, land use (percent farmland, forest, and urban settlement), and dump site density. Elevation and sheep population density were found to be non-significant in this analysis.

Boyd (1997) analyzed landscape attributes selected by six colonizing wolves that dispersed from protected refugia into northwestern Montana, southeastern British Columbia, and southwestern Alberta. Wolves selected landscapes with relatively low elevations, flatter terrain, and closer proximity to water and roads than expected based on availability inside and outside their new home ranges. A logistic regression model was derived using elevation, slope, and distance to roads to predict wolf presence in areas of potential colonization.

A modified "least-cost path" model of landscape connectivity was used to identify critical barriers to dispersal in Banff National Park (Paquet et al. 1997). The least-cost path can be modeled in GIS (geographic information systems) as a combination of the attraction to preferred habitats minus energetic costs (due to topography, snow depth, etc.), security costs (exposure to humans or roads), and physical impediments to movement (Paquet et al. 1997). The Banff study used a time-series analysis to project effects of increased development and road creation on landscape connectivity. Dynamic diffusion models also have been developed using road density and vegetation type to simulate wolf dispersal in U.S. Rockies (Walker and Craighead 1998).

Boyce (1992b, 1995a) developed a simulation model based on stochastic difference equations to explore wolf-prey interactions in the Greater Yellowstone Ecosystem (GYE). This was a "psuedospatial" model in that separate models for three areas in the GYE were created and linked by dispersal. The main prey species for wolves in the GYE are elk, mule deer, moose, and bison. In this model, both hunter harvest and climate influenced prey populations. When human-caused mortality was held constant in the model, the effect of elk population dynamics dominated wolf population dynamics. Elk population dynamics were in turn dominated by the density-independent effects of winter severity, although summer forage production also was important. Although not directly applicable to map-based conservation planning, this type of model affords qualitative insights concerning predator-prey interactions.

Haight et al. (1998) used a simulation model to analyze wolf population dynamics in a semi-developed landscape. They found that low levels of immigration allowed the persistence of isolated wolf populations inhabiting the landscape matrix. Wolves can inhabit areas with high levels of mortality risk (40%) if either spatial refugia (protected populations) exist or if dispersal is possible between buffer populations. This suggests that regional planning incorporating core, buffer, and dispersal can increase habitat the effective size of reserves and allow the distribution of wolves to expand to include much of the landscape matrix (Fritts and Carbyn 1995, Craighead et al. 1997). This message and the limited size of existing protected areas have led several authors to stress the importance of cross jurisdictional planning (Salwasser et al. 1987, Bath et al. 1988, Mladenoff et al. 1995, Boyd et al. 1995, Paquet and Hackman 1995).

We can divide components of wolf habitat models into biological attributes and human-associated disturbance factors. Because of the wolfs' inherent behavioral variability, it is unlikely that all wolves react equally to human-induced change. Moreover, many extraneous factors contribute to variance in behavior of individual wolves. Because we have developed no reasonable expression of those differences, assessment is best applied at the pack and population levels. Solitary individuals (i.e., lone wolves) may show different habitat associations than packs.

APPENDIX B

Connecting Linkages (Corridors)

Many ecologists believe we can reduce the adverse effects of human disturbance with the maintenance or provision of landscape linkages among subpopulations. Much recent literature in conservation biology supports the idea of providing "corridors" of suitable habitat between population centers (Forman and Godron 1986, Harris and Gallagher 1989, Noss 1993). Corridors provide travel lanes to accommodate daily, seasonal, and dispersal movements from one large habitat block to another. In theory, corridors greatly reduce the possibilities of inbreeding and chance environmental catastrophes by providing opportunity for the introgression of new genetic materials and the exchange of individuals from source populations.

Wildlife movement corridors facilitate the biologically effective transport of animals between larger patches of habitat. Corridors are linear habitats whose primary wildlife function is to connect two or more significant habitat areas. Although corridors may have intrinsic wildlife value, their salient value is that they connect more substantive patches of habitat. Corridors generally are used to maintain connectivity among formerly contiguous wildlands, not to connect naturally isolated units. Conservation theory suggests that by protecting landscape linkages between the remaining patches of habitat, we can prevent or forestall the future loss of species, but at population levels lower than in pristine conditions. When human activities threaten to disrupt natural patterns of wildlife movement, we must take measures to avoid impacts or create a wildlife movement corridor out of another area.

We can categorize most species into one of two types of corridor users. "Passage species" need corridors to allow individuals to pass directly between two areas in discrete events of brief duration (e.g., dispersal of a juvenile, seasonal migration, or moving between parts of a large home range). For passage species, corridors may function as transitional habitats that provide only those ecological services and resources required when individuals move between patches. Large herbivores and medium to large carnivores are typically passage species, as are many migratory animals. These species do not have to meet all of their life requirements within the corridor, but the corridor must provide conditions that motivate the animal to enter and use the corridor. In other cases, corridors may comprise habitats that are critical for day to day survival. In contrast to passage species, "corridor dwellers" need several days to several generations to pass through the corridor (e.g., plants, insects, amphibians, and small mammals).

In pristine conditions, wildlife movements are the product of the individual or group's search for life requisites. Species adaptations, population size, demographic structure, interspecific relations, the abundance and distribution of food, availability of habitat for security, physiography, climate, disturbance activities, and wildlife management actions affect movements. Moreover, some movements seem learned behaviors. In unaltered environments, large mammals move between preferred habitats in response to seasonal forage availability and stages in their life cycle. There is, for example, good evidence that among long-lived species such as wolves or bears (*Ursus sp.*), knowledge of travel routes is passed down by tradition from generation to generation (Mech 1970, Curatolo and Murphy 1986, Thurber et al. 1994, S. Herrero pers. comm., S. Minta pers. comm.).

Ecological factors that determine the availability and quality of wildlife corridors are dynamic and these elements can be expected to change seasonally and among years. Corridors appear to follow "paths of least resistance" (e.g., topography and habitat) that have greatest visibility and fewest obstructions. Corridors seem to be established along routes characterized by low disturbance and escape terrain. Observed travel routes for wolves include human trails, wildlife trails, ridges, open edges, riparian valley bottoms, shorelines, open forest, and roads. Major river and creek valleys, and interconnecting passes, function as local and regional travel corridors (Paquet 1993).

Studies have shown that the width of a corridor is particularly important to allow for unimpeded movement of wildlife. Whereas narrow corridors may work well for small mammals and some bird species, corridors several kilometers in width may be necessary for use by large mammal species such as wolves (Harrison 1992, Merriam and Lanoue 1990). The width required for a corridor to be effective may depend upon its length. Effective corridors may be narrow if they are short enough that dispersers may pass through without foraging.

In human dominated landscapes, competing land uses that may directly or indirectly conflict with species requirements limit the availability and quality of movement corridors. The presence of human facilities (physical impediments) along natural routes may displace wildlife from traditional paths, force them to adopt alternative routes, or lead to permanent abandonment of habitat that was once contiguous or connected by the route. Obstructions to movements may be physical or psychological, consisting of physical impediments, sensory impediments, and the loss of forest cover in travel corridors and in adjacent areas. For example, divided highways ≥ 90 m wide were considered the equivalent of bodies of water twice as wide in obstructing movements of small forest animals (Oxley et al. 1984). Concrete embankments, highway fences, urban communities, and motor vehicle traffic were barriers to cougar movement in Southern California (Beier in press, via K. Heuer pers. comm.). Many animals perceive darkness as a form of cover, travelling in open areas during the night. Wolves in Italy, for example, living in a densely populated and highly fragmented landscape shifted to nocturnal behavior to avoid humans (Boitani 1982). Night lighting was identified as a factor that compromised the potential effectiveness of a corridor for cougars in Southern California (Beier in press, via K. Heuer pers. comm.).

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