Habitat Fragmentation and Interspecific Competition: Implications for Lynx Conservation

Steven W. Buskirk, Department of Zoology and Physiology, University of Wyoming, P.O. Box 3166, Laramie, WY 82071

Leonard F. Ruggiero, Rocky Mountain Research Station, 800 E. Beckwith, P.O. Box 8089, Missoula, MT 59807

Charles J. Krebs, Department of Zoology, University of British Columbia, 6270 University Blvd., Vancouver, BC V6T 1Z4 Canada

Abstract—Habitat fragmentation and interspecific competition are two important forces that potentially affect lynx populations. Fragmentation operates by various mechanisms, including direct habitat loss, vehicle collisions and behavioral disturbance from roads, and changes in landscape features such as edges. Competition takes two forms: Exploitation competition involves potential competitors, such as coyotes and raptors, for food with lynx. Interference competition involves aggressive acts, almost always by a larger animal, that can include attacking and killing. Habitat fragmentation tends to facilitate competition by generalist predators, of which the most likely beneficiary is the coyote. Other potential interference competitors with lynx include cougars and bobcats. Of these three carnivores, all are more widespread and more abundant within the southern distribution of the lynx than 50 years ago.

Introduction

Fragmentation (Dayan et al. 1989) and competition (Rosenzweig 1966) are major forces shaping the evolution, composition, and function of carnivore communities ("carnivorans" is a more precise term referring to members of the Order Carnivora; we use "carnivoran" and "carnivore" synonymously). In human-dominated landscapes, fragmentation and competition are strongly linked because vegetation mosaics in landscapes provide high quality environments for generalist species such as the coyote and great-horned owl (Goodrich and Buskirk 1995). Under such conditions, generalist predators are favored over habitat specialists such as the spotted owl and American marten. As humans change the patterns of natural landscapes through timber harvest, construction of roads and buildings, and conversion of land to other uses, ecological processes such as competition, dispersal, and predation are affected in various ways (Wilcove 1985). Although many of these effects are poorly understood, it is clear that the structure and function of animal communities can be dramatically altered (Wilcove et al. 1986; Yahner 1988; Oehler and Litvaitis 1996). Here, we discuss how interspecific competition affects carnivores in general, how habitat fragmentation may mediate this process, and how lynx populations in particular may be affected.

Habitat Fragmentation

The term "fragmentation" is used widely to describe human alterations of natural landscapes (Knight et al., in press). Lord and Norton (1990) defined this process as the disruption of continuity, especially as it relates to ecosystem processes. Forman (1995) discussed how fragmentation affects the area, size, shape, and configuration of landscape elements, in an overall process of land transformation that has major implications for conservation (Lord and Norton 1990; Wilcove et al. 1986). Fragmentation has been variously defined to describe a reduction of total area, increased isolation of patches, and reduced connectedness among patches of natural vegetation (Rolstad 1991). Fragmentation tends to reduce habitat area and to isolate patches of native vegetation (especially in late seral stages) from each other, both of which can lead to local species extirpations (Wilcox 1980; Wilcox and Murphy 1985). Moreover, the loss of some species in this way can lead to multiple extinctions through community-level secondary effects (Wilcox and Murphy 1985).

Fragmentation has been applied to both natural (Andrén 1994) and human-caused alterations of landscape patterns. Here, we use the term "patchiness"

when referring to natural processes (Buskirk et al., in press) and "fragmentation" to anthropogenic disruption of natural patterns and the secondary effects of such disruption (e.g., behavioral disturbance to wildlife), and the effects of cars, pets, garbage, and other human accoutrements (Buskirk et al., in press).

Although appropriate to any landscape, fragmentation has been preferentially applied to forests (Simberloff 1994; Lehmkuhl and Ruggiero 1991; Harris 1984). In this context, some have argued that the negative effects of forest fragmentation are ameliorated in areas like the Rocky Mountains because of naturally patchy landscapes. This contention is unlikely to be true given that, by definition, fragmentation disrupts the natural landscape pattern regardless of the scale of the undisturbed pattern. That is, fragmentation is not scale-limited (Lord and Norton 1990). Moreover, natural landscape pattern is a complex function of topography with its associated (e.g., edaphic, microclimatic) gradients and natural disturbance processes, the most important of which is fire. Clearly, the kinds, amounts, and arrangements of forested environments differ markedly between natural and anthropogenic disturbances (Harris 1984; Ruggiero et al. 1991).

Fragmentation has been shown to affect a fairly wide range of birds and mammals (reviewed by Harris 1984, Bright 1993, Andrén 1994, and Oehler and Litvaitis 1996). This is not surprising, considering the wide range of mechanisms whereby vertebrates can be impacted—for example, loss of area, isolation of patches, vehicle collisions, increased predation by edge-preferring predators, changes in boundary conditions including altered moisture regimes near stand edges, and changes in the habitat matrix or context within which undisturbed habitats exist. Several of these mechanisms can mediate competitive relationships by permitting generalist predators such as coyotes access to landscapes occupied by specialist species that are ecologically separated in natural landscapes (Hunter 1990). Moreover, our considerable understanding of ecological systems and mechanisms of competition provides a plausible basis for believing habitat-mediated competition is an important factor in population persistence. Finally, as clearly stated by Wilcox and Murphy (1985:884), "That current ecological theory is inadequate for resolving many of the details should not detract from what is obvious and accepted by most ecologists: habitat fragmentation is the most serious threat to biological diversity and is the primary cause of the present extinction crisis."

Direct habitat effects of fragmentation of most concern in lynx conservation are (1) reduction of area and patch size of late-successional forest and of optimal snowshoe hare habitat; (2) creation of openings that facilitate access by potentially competing carnivores; (3) increased densities of edges

between early successional and other forest types; and (4) changes in the amounts and structural complexity of seral forest stands within landscapes. Although landscape-level studies have not determined how fragmentation affects lynx ecology and population persistence (Koehler and Aubry 1994), rare species associated with wilderness, such as the lynx, generally are considered most susceptible to fragmentation (Bright 1993). Likewise, habitat specialists with large individual spatial needs, including the lynx (Quinn and Parker 1987; O'Donoghue et al. 1998), are likely to be impacted by habitat fragmentation (Andrén 1994). This is so because generalist predators tend to dominate the predator guild in fragmented landscapes (Oehler and Litvaitis 1996).

Competition

Keddy (1989:2) defined competition as "the negative effects which one organism has upon another by consuming, or controlling access to, a resource that is limited in availability." Two qualitatively different kinds of interspecific competition can be illustrated by examples involving the lynx (Fig. 4.1).

Exploitation (resource) competition (Litvaitis 1992) occurs when other species, such as the northern goshawk, bobcat, or coyote, use resources that limit the fitness of a lynx. Thus, if northern goshawks exploit snowshoe hares in an area so thoroughly that lynx die sooner (from starvation or while dispersing to a new place), breed less (from females failing to mate or give birth), or produce smaller litters of kittens than they would otherwise, we say that northern goshawks competed (exploitatively) with lynx. Although the competition might have been reciprocal, that issue is academic from our perspective here.

Interference competition (Case and Gilpin 1974) occurs when one species acts aggressively toward another, denying it access to a resource (Fig. 4.1). For example, if a cougar were to chase a lynx away from a hare carcass, or kill one of its kittens, or scent mark an area so that lynx were deterred from foraging there, this would constitute interference competition. Exploitation competition is not particularly affected by the relative body sizes of the participants, as in the hypothetical example of the smaller goshawk and the larger-bodied lynx. Interference competition, by contrast, is almost invariably inflicted by a larger carnivore on a smaller one (Fig. 4.2). Further, the likelihood of interference competition among carnivores seems to be greatest when two species are similar in body form and size (Buskirk in press); for example, wolves are more likely to exert interference competition on coyotes than on red foxes (similar shape but different size: Johnson and Sargeant 1977) or on badgers (different shape).
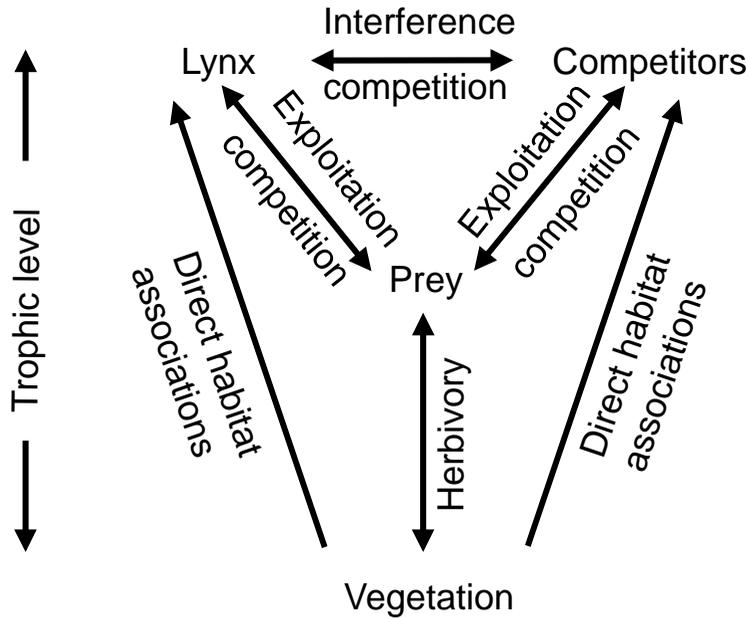
Figure 4.1—Competitive, trophic, and habitat relationships involving lynx. Interference competition, when it involves killing, can include ingestion. Direct habitat associations refer to needs of animals and constraints imposed by physical structure such as live vegetation, coarse woody debris, and snow.
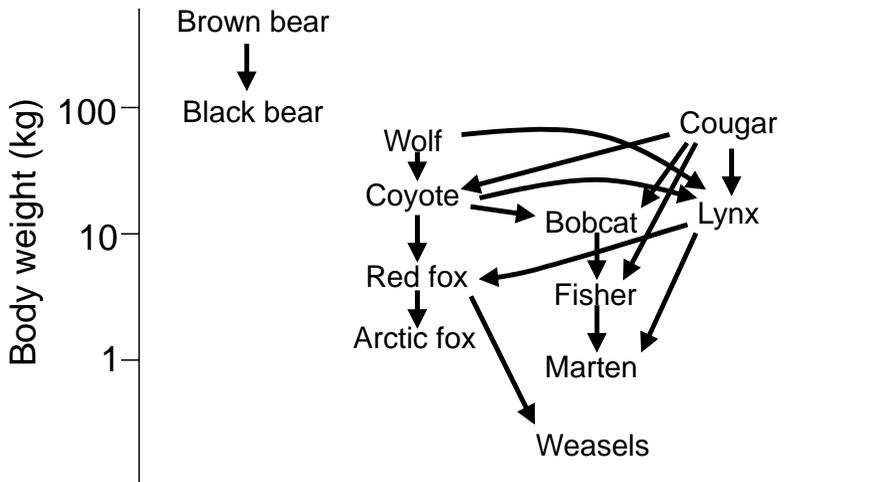

Figure 4.2—Interference competitive interactions among North American carnivores. Arrows point from dominant to subordinate participant and in all cases point downward on the body-weight axis. Interactions are documented in Litvaitis (1992), Buskirk (1999), and this chapter.

Interference competition appears to be capable of influencing carnivore populations to remarkable degrees. Although exploitation competition can reduce prey abundance and thus cause predators to become rare (the numerical response: Taylor 1984), interference competition can drive them to local or regional extinction. For example, Ashbrook and Walker (1925) described how one red fox eradicated all (at least six) of the arctic foxes on Chowiet Island, Alaska (56° 2' N., 156° 40' W., 0.8 km^2 in area) in less than three years. Similarly, wolves on Isle Royale, Michigan (Krefting 1969) and the Kenai Peninsula, Alaska (Thurber et al. 1992) have been credited with eradicating coyotes upon arrival in the former area and with preventing their sympatry before the extinction of wolves of the latter area. The potentially high importance of interference competition, compared with exploitation competition, is surprising unless one considers the prey-switching ability that is a common adaptation of carnivores (Taylor 1984). Alternate prey can allow carnivores to persist when preferred prey are scarce, but an effective interference competitor can pursue its enemy to scarcity or extinction. Thus, interference competition and prey availability are both critically important issues in the distribution and abundance of mesocarnivores, including the lynx.

The effects of fragmentation on predator-prey interactions (and thus perhaps interference competition) depend on the specific behaviors of the species in question (Kareiva 1987) and its environment. Thus, predation and competition are highly context-specific phenomena. Various biotic and abiotic factors can mediate competitive interactions (direct habitat associations, Fig. 4.1), so that a dominant competitor in one setting coexists or is subordinate in another (Sargeant et al. 1987). Many such mediated relationships have been reported. In carnivores, for example, Paquet (1991) reported that coyotes did not avoid wolves during winter, and Gese et al. (1996) concluded that coyotes tolerated red foxes in Yellowstone National Park during a high prey year, but not at other times. A strong abiotic affect on interactions between another pair of forest-dwelling carnivores, the marten and fisher, has been described by Krohn et al. (1995). Martens, with their proportionally larger feet, can travel in deeper, softer snow than can fishers, and martens predominate in parts of Maine with deep soft snow. But, fishers are competitively (interference) dominant over martens, and therefore are the more common species where snow is shallow or crusted.

We summarize possible relationships between lynx and potential competitors in Table 4.1 and Figure 4.2. As discussed earlier, direct evidence of competition is very difficult to collect and therefore scarce. The fact that there have been very few intensive studies of lynx in the United States contributes to the lack of empirical information. In some cases, exploitation of a common

Table 4.1—Possible competitive impacts to lynx, mediating factors, and our evaluation of the likely importance of the causes in the decline of lynx in the contiguous United States.

Possible impact	Potential competitors	Likely importance
Exploitation (food)	Birds of prey (goshawk and great-horned owl)	Minimal impact
	Coyote	Locally or regionally important
	Wolf	Minimal impact
	Cougar	Minimal impact
Interference	Coyote	Possible
	Bobcat	Possible where bobcats occupy high-elevation habitats
	Wolverine	Documented, but likely rare
	Cougar	Likely in summer or where lynx venture out of deep snow areas

prey species (e.g., snowshoe hares) and numerical (great-horned owl - Rohner and Krebs 1996, 1998) or functional (red-tailed hawk - Adamcik et al. 1979) responses to increasing hare abundance serves to indicate potentially important competitive relationships. For predators such as the great-horned owl, a functional response to hare abundance could lead to owl predation on lynx kittens, although this has not been reported (C. Rohner, personal communication). Thus, functional responses to increased prey abundance may have the primary effect of increased exploitation competition and a secondary or indirect effect of increased interference competition.

Competition With Cougars

Interference competition between cougars and bobcats was reported by Koehler and Hornocker (1991), who found that cougars killed bobcats when both species were forced to lower elevations in winter. Squires and Lorean (Chapter 11) document two lynx killed by cougars in western Montana during fall and early winter. Based on these observations and because cougars are larger than lynx and have become more abundant in the western United States in recent years (Green 1991), cougars may be significant interference competitors with lynx. Deep snow, however, is a hindrance to cougar movements (Fig. 4.3), and should spatially separate lynx and cougars under normal winter conditions. Strong demographic consequences of interference have been reported for another pair of felids, the cheetah and African lion. Caro and Laurenson (1994) reported that lions killed entire cheetah litters, contributing to a survival rate at age two months of 29%. Such killing of litters has not been reported for lynx. Other carnivores,
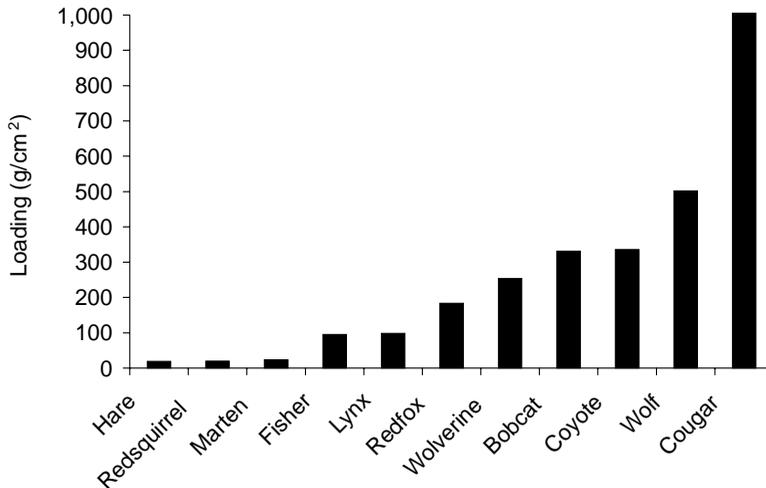
Figure 4.3—Foot loadings of North American mammals important as prey and community associates of Canada lynx. Weights were taken from Chapman and Feldhamer (1982) and Silva and Downing (1995). Foot surface areas were estimated for the larger foot of each species by first enlarging the drawings of tracks in snow depicted in Forrest (1988) so that their length was the mid-range reported by Forrest (1988). The area of the track (cm²) was then measured by digital planimetry (Tamaya Digital Planimeter). Foot loading is an approximation of the pressure exerted by the animal walking on snow, and therefore its sinking depth. High sinking depth suggests that, other factors being equal, an animal exerts more energy to traverse snow while walking. The snowshoe hare has the lowest foot loading of any mammal considered, the cougar the highest.

including wolverines and feral dogs (reviewed by McCord and Cordoza 1982 and Quinn and Parker 1987), occasionally kill or take food from lynx.

Competition With Bobcats

Bobcats attain larger body size than lynx (Hall 1981) and may be larger than sympatric lynx in some areas. Among a small sample of sympatric bobcats and lynx in western Wyoming, the largest male bobcat was 2-4 kg larger than the largest male lynx (T. Lorean, personal communication). Such a body-size difference would set the stage for interference competition dominated by bobcats. Further, the diets of both species (reviewed by Rolley 1987 and Quinn and Parker 1987) tend to be dominated by leporids, creating the potential for exploitation competition. Where bobcats attain high densities and body sizes larger than those of sympatric lynx, competitive impacts upon lynx should be suspected. Although bobcats and lynx are generally thought to be ecologically separated by deep snow, interactions between

these two species under other conditions are poorly understood. For example, in Montana, Smith (1984) reported that bobcat home ranges during winter were located at significantly lower elevations than were lynx home ranges, but that this difference disappeared during spring and autumn. Similarly, in western Maine, Major (1983) found that snowshoe hares ranked first or second in frequency of occurrence in bobcat diets during all seasons over a three-year period. Toweill (1986) found that bobcats in the western Oregon Cascades ate snowshoe hares regularly. These findings indicate that bobcats may be significant competitors with lynx under some conditions. That lynx can be excluded by bobcats is suggested by Parker et al. (1983), who believed that bobcats, recent immigrants to Cape Breton Island, caused the displacement of lynx from low areas. These accounts suggest the potentially important influence of bobcats on lynx.

Competition With Coyotes and Wolves

The coyote, because of its wide habitat niche, heavy predation on snowshoe hares (O'Donoghue et al. 1998), high reproductive rate (Quinn and Parker 1987), great behavioral plasticity (Murray and Boutin 1991), and high tolerance of humans (Litvaitis 1992), must be considered a potentially formidable competitor with mesocarnivores, including the lynx. Indeed, coyotes are suspected in various declines of mesocarnivores, as evidenced by documented cases of coyotes competing with or preying on sensitive and endangered species (reviewed by Litvaitis 1992 and Goodrich and Buskirk 1995).

The distribution of coyotes has expanded dramatically during the past few decades, especially to the northeast (Fuller and Kittredge 1996), but also to the northwest. Coyote numbers have increased dramatically in New England, as indexed by numbers of coyotes caught by trappers in New Hampshire (Fig. 4.4). Virtually no coyotes were trapped in New Hampshire before 1970, but coyotes were common by the mid-1970s and continued to increase through the mid-1990s. Pelt price, a strong predictor of harvest of many furbearers, explains little of the increase in coyote harvests in New Hampshire over this period (Fig. 4.4). Similarly, coyote harvests from Washington increased from the five-year period ending 1964-1965 (mean = 362/year) to the five years ending 1983-1984 (mean = 16,250/year; Novak et al. 1987). Consistent with this, coyotes were rare or nonexistent in coniferous forests of the Oregon and Washington Cascades until timber wolves were extirpated around 1930 (Ozoga and Harger 1966).

The ecology of coyotes suggests further that they should be potent competitors. Coyotes at times kill lynx (O'Donoghue et al. 1995), probably most often when lynx are young or in poor condition. O'Donoghue (1997) also
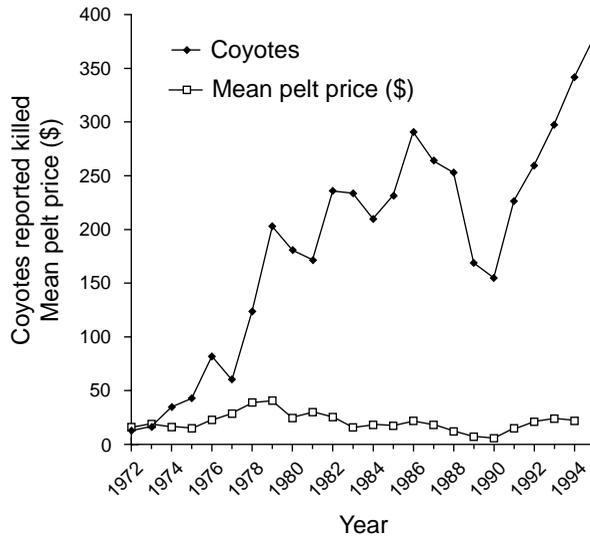
Figure 4.4—Abundance of coyotes in New Hampshire, as indexed by numbers killed in the State and sealed by the State of New Hampshire Game and Fish Department (unpublished data) and mean price paid per pelt to trappers for coyote pelts, as indexed by the same agency (unpublished data). Price is plotted because of the strong influence of price on harvest effort. The year - coyote correlation was r (Pearson) = 0.77, whereas the price - coyote correlation was r = 0.03. Therefore, we conclude that the strong upward linear trend in coyotes killed is the result of their increased abundance.

showed that, comparing densities of lynx, hares, and coyotes between his Yukon study area and that of Keith et al. (1977) in central Alberta, lynx were more abundant where coyotes were less dense, rather than where hares were more dense. Thus, interactions with coyotes appear to influence lynx more than availability of snowshoe hares, generally considered to be the limiting factor for lynx numbers. Similarly, coyotes compete with bobcats in various settings (Nunley 1978; Litvaitis and Harrison 1989). Interference competition (direct killing) of bobcats by coyotes has been documented by Anderson (1986), Jackson (1986), and Toweill (1986), and coyotes have been implicated in bobcat declines in some areas. Considering that bobcats can be larger and are more aggressive than lynx, coyote predation on bobcats suggests the potential for strong interference competition between coyotes and lynx. As with cougars and lynx, this potential likely is the greatest during low-snow periods—the season for which our understanding of lynx ecology is the weakest. Further, coyotes prey primarily on leporids (Voigt and Berg 1987);

within the range of the lynx, coyotes prey heavily on snowshoe hares (Todd et al. 1981; Todd and Keith 1983; Parker 1986; O'Donoghue et al. 1998), and attain high densities (up to 0.44/km², Todd et al. 1981) when snowshoe hare populations are high. O'Donoghue et al. (1998) found that in Yukon Territory coyotes preyed on snowshoe hares during snowshoe hare highs at a higher rate than the lynx predation, suggesting potentially important exploitation competition with lynx. Further, coyote abundance tracked that of snowshoe hares through the cycle much as did lynx, enough that coyotes contributed to the cyclic dynamics of snowshoe hare populations (O'Donoghue et al. 1997). In a similar way, coyote densities have tracked those of snowshoe hares in forest habitats in the contiguous United States during the 1990s (Montana Department of Fish, Wildlife and Parks, unpublished data; Fig. 4.5), which probably is attributable to switching of habitats and prey by coyotes, corresponding with hare population changes. This illustrates the strong prey- and habitat-switching abilities of the coyote (reviewed by Patterson et al., in press), which contribute to its success as a competitor.
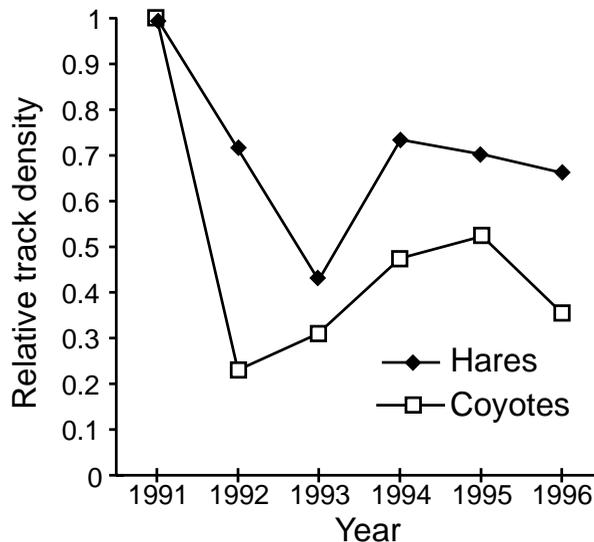

Figure 4.5—Relative abundance of coyotes and snowshoe hares on transects in Montana, 1991 to 1996. The correlation between hare and coyote track densities, without any time lag, is significant ($r = 0.81$, $df = 4$, $P = 0.05$). The absence of a lag in the correlation suggests that the relationship is at least partially due to habitat and prey switching by coyotes in response to fluctuating hare densities.

Numerous reports describe coyotes accessing high-elevation, deep snow areas by moving along paths, roads, and snowshoe hare trails (Bider 1962; Ozoga and Harger 1966; Murray et al. 1995). Unpublished data from Oregon (USDA Forest Service, unpublished report) and Colorado (Byrne 1998, unpublished) also suggest that coyotes use high elevation areas, although their means of access is not known. Byrne (1998, unpublished) conducted track surveys for snowshoe hares and recorded other species' tracks on 1,160 km of snow transects within presumed snowshoe hare habitat (7,500-11,800 feet elevation) in winter. Coyotes were the second most common carnivore taxon (after weasels) encountered, with 628 tracks recorded. The elevation zone with the highest frequency of coyote tracks was 8,000-9,000 feet but coyote tracks were fairly common (about 0.45/km of transect) in the 9,000-10,000 and 10,000-11,000 foot elevation zones. These results indicate that coyotes are much more common in high elevation, deep snow areas of western mountains than generally has been believed to be the case.

Nevertheless, some basis exists to believe that coyotes and lynx are spatially segregated in winter by deep snow. In central Alberta, Todd et al. (1981) found that coyote use of open habitats increased from November to March, which they attributed to snow accumulation in forest and the greater compactness and load-bearing strength of snow in openings. This intolerance of deep snow resulted in a diet shift from snowshoe hares to ungulate carrion in winter. Also in Alberta, Murray et al. (1994) found that coyotes were more selective of hard or shallow snow conditions than were lynx. In the western (Murray and Boutin 1991) and northeastern United States (Litvaitis 1992), this morphological difference causes coyotes and lynx to be spatially segregated by snow conditions. In the West, this occurs along an elevational gradient. Such separation should minimize competition between the two species. However, this separation may break down where human modifications to the environment increase access by coyotes to deep snow areas. Such modifications include expanded forest openings throughout the range of the lynx in which snow may be drifted, and increased snowmobile use in deep snow areas of western mountains. Recreational snowmobile use has expanded dramatically in the contiguous United States in the past 25 years, with hundreds of thousands of km of trails (>19,000 km of groomed trails in Maine alone) within the pre-settlement range of the lynx (Maine Snowmobile Association, World Wide Web site, Zesiger 1997). Various unpublished accounts describe snowmobile and snowshoe trails facilitating access by coyotes to areas used by hares and lynx. In the Yukon, coyotes use both snowshoe and snowmobile trails (O'Donoghue, personal communication). This facilitation of travel, in general, could help explain

possible lynx reductions in the West via human-facilitated competition from coyotes and other generalist predators. Better understanding of this postulated relationship is critical.

Although wolves have been reported to kill lynx, only for Fennoscandia is there evidence that wolves exert population-level interference competition with lynx (Pulliainen 1965). We suspect that a more likely effect of wolves on lynx is by reducing numbers of coyotes, one of the strongest examples of fierce interference competition among carnivores (Buskirk 1999). In a few areas of the contiguous United States, wolves are becoming more common and coyotes more scarce. Lynx should fare better with sympatric wolves than with sympatric coyotes, because wolves prey little on leporids (Mech 1970) and are marginally too large to be interference competitors with lynx (Fig. 4.2). We predict that the Greater Yellowstone Area and northern Montana, with expanding wolf and shrinking coyote populations, will increase their suitability for occupancy by lynx in coming years.

Conclusions

Fragmentation of habitats occupied by lynx (including increased openings, higher road densities, exurban residential development, and wider use of snowmobiles and devices that compact snow in areas with deep, soft snow) is a plausible mechanism for the questionable conservation status of the lynx in the contiguous United States. Competition could take the form of exploitation by other predators of snowshoe hares, particularly the coyote, or involve interference competition, with larger-bodied carnivores acting aggressively toward lynx, even killing them. The coyote, because of its broad niche tolerances, high reproductive rate, and expanding range in the contiguous United States, is particularly suspect in competition. In spite of this evidence suggesting that coyotes may exploitatively compete with lynx, we suspect that, at least where hare populations cycle, exploitative competition impacting lynx is unlikely. Competitive systems involving cycling snowshoe hares never come to equilibrium and the primary impact of the competition should be overwhelmed by the large changes in prey availability. Even so, in the southern part of the range of lynx, if hares fluctuate less dramatically than they do in the North, exploitation competition inflicted by coyotes may reduce lynx numbers. Overall, we suspect that interference competition is more likely to be the critical form of competition that needs to be evaluated for lynx in the contiguous United States. Cougars, in particular, appear to be effective interference competitors with lynx.

Literature Cited

Adamcik, R. S., A. W. Todd, and L. B. Keith. 1979. Demographic and dietary responses of red-tailed hawks during a snowshoe hare fluctuation. Can. Field-Nat. 93:16-27.

Anderson, E. M. 1986. Bobcat behavioral ecology in relation to resource use in southeastern Colorado. Ph.D. Diss., Colorado State University, Fort Collins.

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355-366.

Ashbrook, F. G. and E. P. Walker. 1925. Blue fox farming in Alaska. USDA Bulletin No. 1350.

Bider, J. R. 1962. Dynamics and the temporo-spatial relations of a vertebrate community. Ecology 43:634-646.

Bright, P. W. 1993. Habitat fragmentation - problems and predictions for British mammals. Mammal Review 23: 101-111.

Buskirk, S. W. 1999. Mesocarnivores of Yellowstone. Pages 165-187 in Clark, T. W., S. C. Minta, P. M. Kareiva, and P. M. Curlee, editors. Carnivores in ecosystems. Yale University Press, New Haven, CT.

Buskirk, S. W., W. H. Romme, F. W. Smith, and R. L. Knight. In press. An overview of forest fragmentation in the southern Rocky Mountains. in R. L. Knight, F. W. Smith, S. W. Buskirk, W. H. Romme, and W. L. Baker, editors. Forest fragmentation in the southern Rocky Mountains. University Press of Colorado, Boulder.

Byrne, G. 1998. A Colorado winter track survey for snowshoe hares and other species. Unpublished report, Colorado Division of Wildlife, Glenwood Springs, CO.

Caro, T. M. and M. K. Laurenson. 1994. Ecological and genetic factors in conservation: a cautionary tale. Science 263:485-486.

Case, T. J. and M. R. Gilpin. 1974. Interference competition and niche theory. Proceedings of the National Academy of Sciences 71:3073-3077.

Chapman, J. A. and G. A. Feldhamer. 1982. Wild mammals of North America. Johns Hopkins University Press, Baltimore, MD. 1147.

Dayan, T., D. S. Simberloff, E. T. Chernov, and Y. Yom-Tov. 1989. Inter- and intra-specific character displacement in mustelids. Ecology 70:1526-1539.

Forman, R. T. T. 1995. Land mosaics: the ecology of landscapes and regions. Cambridge University Press, Cambridge, UK.

Forrest, L. R. 1988. Field guide to tracking animals in snow. Stackpole Books, Harrisburg, PA.

Fuller, T. K. and D. B. Kittredge, Jr. 1996. Conservation of large forest carnivores. Pages 137-164 in R. M. DeGraaf and R. I. Miller, editors. Conservation of faunal diversity in forested landscapes. Chapman and Hall, London, UK.

Gese, E. M., T. E. Stotts, and S. Grothe. 1996. Interactions between coyotes and red foxes in Yellowstone National Park, Wyoming. Journal of Mammalogy 77:377-382.

Goodrich, J. M. and S. W. Buskirk. 1995. Control of abundant native vertebrates for conservation of endangered species. Conservation Biology 9:1357-1364.

Green, K. A. 1991. Summary: mountain lion - human interaction questionnaires, 1991. Unpublished abstract, Mountain lion - human interaction workshop. Colorado Division of Wildlife, Denver, CO.

Hall, E. R. 1981. The mammals of North America. John Wiley and Sons, New York, NY.

Harris, L. D. 1984. The fragmented forest: island biogeography theory and the preservation of biotic diversity. University of Chicago Press, Chicago, IL.

Hunter, M. L., Jr. 1990. Wildlife, forests and forestry. Prentice Hall, Englewood Cliffs, NJ.

Jackson, D. H. 1986. Ecology of bobcats in east-central Colorado. Ph.D. Dissertation, Colorado State University, Fort Collins, CO.

Johnson, D. H. and A. B. Sargeant. 1977. Impact of red fox predation on the sex ratio of prairie mallards. U.S. Fish and Wildlife Service, Wildlife Research Report 6.

Kareiva, P. 1987. Habitat fragmentation and the stability of predator-prey interactions. Nature 326:388-390.

Keddy, P. A. 1989. Competition. Chapman and Hall, New York, NY.

Keith, L. B., A. W. Todd, C. J. Brand, R. S. Adamcik, and D. H. Rusch. 1977. An analysis of predation during a cyclic fluctuation of snowshoe hares. Proceedings of the International Congress of Game Biologists 13:151-175.

Knight, R. L., F. W. Smith, S. W. Buskirk, W. H. Romme, and W. L. Baker. In press. Forest fragmentation in the southern Rocky Mountains. University Press of Colorado.

Koehler, G. M. and K. B. Aubry. 1994. Lynx. Pages 74-98 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski, editors. The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine in the western United States. USDA Forest Service, General Technical Report RM-254.

Koehler, G. M. and M. G. Hornocker. 1991. Seasonal resource use among mountain lions, bobcats and coyotes. Journal of Mammalogy 72-391-396.

Krefting, L. W. 1969. The rise and fall of the coyote on Isle Royale. Naturalist 20(3):24-31.

Krohn, W. B., K. D. Elowe, and R. B. Boone. 1995. Relations among fishers, snow and martens: development and evaluation of two hypotheses. Forestry Chronicle 71:97-105.

Lehmkuhl, J. F. and L. F. Ruggiero. 1991. Forest fragmentation in the Pacific Northwest and its potential effects on wildlife. Pages 35-46 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, editors. Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service General Technical Report PNW-285.

Litvaitis, J. A. 1992. Niche relations between coyotes and sympatric Carnivora. Pages 73-85 in A. H. Boer, editor. Ecology and management of the eastern coyote. University of New Brunswick Wildlife Research Unit, Fredericton, NB.

Litvaitis, J. A. and D. J. Harrison. 1989. Bobcat-coyote niche relationships during a period of coyote population increase. Canadian Journal of Zoology 67:1180-1188.

Lord, J. M. and D. A. Norton. 1990. Scale and the spatial concept of fragmentation. Conservation Biology 4(2):197-202.

Major, J. T. 1983. Ecology and interspecific relationships of coyotes, bobcats, and red foxes in western Maine. Ph.D. Dissertation, University of Maine.

McCord, C. M. and J. E. Cardoza. 1982. Bobcat and lynx. Pages 728-766 *in* J. A. Chapman and G. A. Feldhamer, editors. Wild mammals of North America. Johns Hopkins University Press, Baltimore, MD.

Mech, L. D. 1970. The wolf: the ecology and behavior of an endangered species. Natural History Press, Garden City, NY.

Murray, D. L. and S. Boutin. 1991. The influence of snow on lynx and coyote movements: does morphology affect behavior? Oecologia 88:463-469.

Murray, D. L., S. Boutin, and M. O'Donoghue. 1994. Winter habitat selection by lynx and coyotes in relation to snowshoe hare abundance. Canadian Journal of Zoology 72:1444-1451.

Murray, D. L., S. Boutin, M. O'Donoghue, and V. O. Nams. 1995. Hunting behavior of a sympatric felid and canid in relation to vegetative cover. Animal Behavior 50:1203-1210.

Novak, M., M. E. Obbard, J. G. Jones, R. Newman, A. Booth, A. J. Satterthwaite, and G. Linscombe. 1987. Furbearer harvests in North America, 1600-1984. Ontario Trappers Association, Ontario, Canada.

Nunley, G. L. 1978. Present and historical bobcat trends in New Mexico and the West. Proceedings of the Vertebrate Pest Conference 8:77-84.

O'Donoghue, M. 1997. Responses of coyotes and lynx to the snowshoe hare cycle. Ph.D. Dissertation, University of British Columbia, Vancouver.

O'Donoghue, M., S. Boutin, C. J. Krebs, and E. J. Hofer. 1997. Numerical responses of coyotes and lynx to the snowshoe hare cycle. Oikos 80:150-162.

O'Donoghue, M., S. Boutin, C. J. Krebs, G. Zuleta, D. L. Murray, and E. J. Hofer. 1998. Functional response of coyotes and lynx to the snowshoe hare cycle. Ecology 79:1193-1208.

O'Donoghue, M., E. Hofer, and F. I. Doyle. 1995. Predator versus predator. Natural History 104:6-9.

Oehler, J. D. and J. A. Litvaitis. 1996. The role of spatial scale in understanding responses of medium-sized carnivores to forest fragmentation. Canadian Journal of Zoology 74:2070-2079.

Ozoga, J. J. and E. M. Harger. 1966. Winter activities and feeding habits of northern Michigan coyotes. Journal of Wildlife Management 30(4):809-818.

Paquet, P. 1991. Winter spatial relationships of wolves and coyotes in Riding Mountain National Park, Manitoba. Journal of Mammalogy 72:397-401.

Parker, G. R. 1986. The seasonal diet of coyotes, *Canis latrans*, in northern New Brunswick. Canadian Field-Naturalist 100:74-77.

Parker, G. R., J. W. Maxell, and L. D. Morton. 1983. The ecology of the lynx (*Lynx canadensis*) on Cape Breton Island. Canadian Journal of Zoology 61:770-786.

Patterson, B. R., L. K. Benjamin, and F. Messier. In press. Prey switching and the feeding habits of eastern coyotes in relation to the densities of snowshoe hare and white-tailed deer. Canadian Journal of Zoology.

Pulliainen, E. 1965. Studies of the wolf in Finland. Ann. Zool. Fenn. 2:215-259.

Quinn, N. W. S. and G. Parker. 1987. Lynx. Pages 683-694 *in* M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, editors. Wild furbearer management and conservation in North America. Ontario Ministry of Natural Resources, Ontario.

Rohner, C. and C. J. Krebs. 1996. Owl predation on snowshoe hares: consequences of antipredator behaviour. Oecologia 108:303-310.

Rohner, C. and C. J. Krebs. 1998. Responses of great-horned owls to experimental "hot spots" of snowshoe hare density. Auk 115:694-705.

Rolstad, J. 1991. Consequences of forest fragmentation for the dynamics of bird populations: conceptual issues and the evidence. Biological Journal of the Linnean Society 42:149-163.

Rolley, R. E. 1987. Bobcat. Pages 671-681 *in* M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, editors. Wild furbearer management and conservation in North America. Ontario Ministry of Natural Resources, Ontario.

Rosenzweig, M. L. 1966. Community structure in sympatric Carnivora. Journal of Mammalogy 47:602-612.

Ruggiero, L. F., K. B. Aubry, A. B. Carey, and M. H. Huff. 1991. Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service General Technical Report PNW-285.

Sargeant, A. B., S. H. Allen, and J. O. Hastings. 1987. Spatial relations between sympatric coyotes and red foxes in North Dakota. Journal of Wildlife Management 51:285-293.

Silva, M. and J. A. Downing. 1995. CRC handbook of mammalian body masses. CRC Press, Boca Raton, FL.

Simberloff, D. 1994. How forest fragmentation hurts species and what to do about it. Pages 85-90 *in* W. W. Covington and L. F. Debano, editors. Sustainable ecological systems: implementing an ecological approach to land management. USDA Forest Service General Technical Report RM-247.

Smith, D. S. 1984. Habitat use, home range, and movements of bobcats in western Montana. M.S. Thesis, University of Montana, Missoula.

Taylor, R. J. 1984. Predation. Chapman and Hall, New York, NY.

Thurber, J. M., R. O. Peterson, J. D. Wollington, and J. A. Vucetich. 1992. Coyote coexistence with wolves on the Kenai Peninsula, Alaska. Canadian Journal of Zoology 70:2494-2498.

Todd, A. W., L. B. Keith, and C. A. Fischer. 1981. Population ecology of coyotes during a fluctuation of snowshoe hares. Journal of Wildlife Management 45:629-640.

Todd, A. W. and L. B. Keith. 1983. Coyote demography during a snowshoe hare decline in Alberta. Journal of Wildlife Management 47:394-404.

Toweill, D. E. 1986. Resource partitioning by bobcats and coyotes in a coniferous forest. M.S. Thesis, Oregon State University, Corvallis.

Voigt, D. R. and W. E. Berg. 1987. Coyote. Pages 344-357 *in* M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, editors. Wild furbearer management and conservation in North America. Ministry of Natural Resources, Toronto, Ontario.

Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology 66:1211-1214.

Wilcove, D. S., C. H. McLellan, and A. P. Dobson. 1986. Habitat fragmentation in the Temperate Zone. Pages 237-256 *in* M. E. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, MA.

Wilcox, B. A. 1980. Insular ecology and conservation. Pages 95-118 *in* M. E. Soulé and B. A. Wilcox, eds. Conservation biology: an evolutionary-ecological perspective. Sinauer, Sunderland, MA.

Wilcox, B. A. and D. D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. American Naturalist 125:879-887.

Yahner, R. H. 1988. Changes in wildlife communities near edges. Conservation Biology 2:333-339.

Zesiger, S. 1997. Zero to sixty in three seconds (cold). Fortune 135(6):178.