Chapter 14

Comparative Ecology of Lynx in North America

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Abstract—Lynx occur across a large geographic area, but have only been studied in a few locations, and this has led to extrapolation of understandings into areas with very divergent ecologies. We discuss ecological differences across the range of lynx, contrasting the patterns of climate, vegetation, disturbance dynamics and succession, and predator/prey relationships. In all these particulars, areas where lynx occur within the contiguous United States diverge from the well-studied areas of the taiga. We caution against uncritical application of ecological understandings derived from the North to southern lynx and we emphasize the potential importance of late-successional forests as habitat for hares, red squirrels, and lynx in the southern part of the range of the lynx.

Introduction

Our limited knowledge of lynx ecology in North America comes from only a few areas across a broad geographic range (Table 14.1). For example, we have much greater knowledge of lynx ecology in the taiga (Chapters 6, 9) than in southern boreal forests (Chapters 7, 13). Similarly, most of what is known about habitats of snowshoe hares comes from the north-central and northeastern United States. Understandings are therefore extrapolated to other sites that have different climatic, topographic, and vegetative conditions. Such extrapolations may be inappropriate in some cases and result in negative consequences for lynx conservation (Chapter 5). The comparative assessment of lynx ecology presented here explores this potential problem and identifies solutions. Although most extrapolations at issue are along a several thousand-kilometer ecological gradient from north to south, we also address extrapolations along the potentially more complex west-east gradient (for example from northeastern Washington to Colorado or from Montana to Maine).

Table 14.1—Frequently cited lynx studies according to topic and geographic area. Quality code describes the emphasis of the study: 1) primary topic of study, 2) major component of study, 3) minor component of study.

Topic	Alaska	Pacific Northwest	Yukon, NWT Alberta, Manitoba	Rocky Mountain Region	Northeastern and Northcentral U. S., and eastern Canada
Habitat relationships	Perham 1995 - 2 Paragi et al. 1997 - 1	Koehler 1990 - 2	Murray et al. 1994 - 1 Poole et al. 1996 - 1	Koehler et al. 1979 - 3 Smith 1984 - 3	Parker et al. 1983 - 3
Population dynamics and reproduction	O’Connor 1984 - 1		Elton and Nicholson 1942 - 1 Nellis et al. 1972 - 1 Brand and Keith 1979 - 1 Quinn and Thompson 1987 - 1 Poole 1994 - 1 Boutin et al. 1995 - 1 Slough and Mowat 1996 - 1 Mowat et al. 1996 - 1 O’Donoghue et al. 1997 - 1 Ranta et al. 1997 - 1 O’Donoghue et al. 1998b - 1	Brainerd 1985 – 2	Parker et al. 1983 - 2
Movements and home range	Kesterson 1988 - 1 Perham 1995 - 1 Bailey et al. 1986 - 3	Brittell et al. 1989 - 2 Koehler 1990 - 1	Carbyn and Patriquin 1983 - 1 Ward and Krebs 1985 - 1 Poole 1994 - 2 Slough and Mowat 1996 - 2	Smith 1984 - 3 Brainerd 1985 - 2 Chapter 11 - 2 Chapter 12 - 1	Saunders 1963b - 1 Mech 1980 - 1 Parker et al. 1983 - 2

(con.)

Table 14.1—Con.

Topic	Alaska	Pacific Northwest	Yukon, NWT Alberta, Manitoba	Rocky Mountain Region	Northeastern and Northcentral U. S., and eastern Canada
Habitat relationships of snowshoe hares	Bailey et al. 1986	Black 1965 Sullivan and Sullivan 1982, 1983, 1988 Koehler 1990, 1991		Adams 1959 Dolbeer and Clark 1975 Wolfe et al. 1982	Conroy et al. 1979 Orr and Dodds 1982 Buehler and Keith 1982 Parker 1984 Litvaitis et al. 1985 Parker 1986 Fuller and Heisey 1986 Monthey 1986 Rogowitz 1988 Scott and Yahner 1989 Thompson et al. 1989 Thompson and Curran 1995 Ferron and Ouellet 1992 St-Georges et al. 1995
Foraging behavior	Stephenson et al. 1991 - 1		Nellis and Keith 1968 Brand et al. 1976 - 2 Ward and Krebs 1985 Murray et al. 1995 O'Donoghue et al. 1998a		
Food habits	Kesterson 1988 - 2 Staples 1995 - 2	Koehler 1990 - 2	van Zyll de Jong 1966 - 1 Brand et al. 1976 - 1 Brand and Keith 1979 - 2 O'Donoghue et al. 1998a,b - 2	Chapter 12 - 2	Saunders 1963a - 1 Parker et al. 1983 - 2
Dispersal		Brittell et al. 1989 - 3	Ward and Krebs 1985 - 2 O'Donoghue et al. 1995 - 3 Slough and Mowat 1996 - 2 Poole 1997 - 1	Mech 1977 - 3 Brainerd 1985 - 3	
Predator and competitor interactions		Koehler et al. 1979 - 3	Murray and Boutin 1991 - 1 O'Donoghue et al. 1995 - (observations)	Chapter 11 - 3	

As the chapters in this book show, the ecological relationships and population dynamics of the lynx show similarities across its range (Chapters 8, 13). However, they also reflect significant differences in the environments occupied by lynx (Chapters 3, 9, 13), suggesting that there may be important geographical differences in lynx ecology. Therefore, we assess the nature and extent of regional variation in key biotic and abiotic gradients that appear to affect the lynx and its prey. We divide the chapter into five sections:

1. Direct climatic effects
2. Natural disturbance regimes, topography, and resulting landscape patterns
3. Forest successional pathways
4. Patterns of snowshoe hare and red squirrel abundance
5. Predator-prey communities

Direct Climatic Effects

Temperature and moisture regimes appear to limit the distribution of lynx at coarse and fine scales via differential effects on snowfall and habitat structure. In the North (Bailey's [1998] Polar Domain), frozen soils and permafrost generally hold water near the soil surface, favoring high densities of shrubs and young trees. Also, cold air holds relatively little moisture, so that snow is only moderately deep and very dry. These conditions are favorable for lynx and snowshoe hares. However, to the south, soil moisture in summer is lower, higher elevation forests experience higher evaporation rates, and mountain ranges cause patterns of soil moisture and snow deposition to be much more localized. Areas of boreal forest are therefore more patchily distributed in the southern part of the species' range (Chapters 3, 8). This may also mean that lynx favor more mesic north-facing aspects farther south, as was found on the Okanogan Plateau of Washington (Chapter 10).

Snow depths in boreal forests and their southern extensions generally increase from north to south, with the deepest snows generally found in southern Colorado. This is because colder northern air holds relatively less moisture than the warmer air farther south (Pruppacher and Klett 1978, Fig. 4.6). On the other hand, snow in southern lynx habitats may undergo more winter thaws, with subsequent formation of crusts, than snow in the taiga. Crusted snow would tend to remove the competitive advantage held by lynx, with their long limbs and low foot loadings (Chapter 4). Such an advantage or the lack thereof may contribute importantly to the success or failure of lynx populations in some parts of their range. Because of the fragmented nature of landscapes and heterogeneous distribution of topographic, climatic, and vegetative conditions in western forests, lynx and snowshoe hare habitats there are more prone to a metapopulation structure, which has important implications for their population ecology (Chapter 2). This condition is exacerbated by the presumably greater human-caused fragmentation of lynx habitat in the south.

In the East, the climax forest condition of deciduous or mixed deciduous/coniferous trees differs sharply from conditions in the West where succession tends toward coniferous trees. This difference is due to variable influences of climate, specifically the frequency of precipitation and the effects of elevation. But, in eastern North America, human influences have been pervasive so that few eastern forests at temperate latitudes are in a climax condition. As a result, many of the eastern forests that were lynx habitat in presettlement times are younger and mostly deciduous-dominated today.

Natural Disturbance Regimes, Topography, and Resulting Landscape Patterns

Successional stage is commonly regarded as a correlate of habitat quality for snowshoe hares and strongly reflects natural disturbance regimes. The taiga is extensive, has fairly homogeneous climate and physiognomy, and exhibits little topographic relief (Elliot-Fisk 1988). Kelsall et al. (1977) described the remarkably uniform snow depths (mean annual total snowfall = 102 -127 cm) across the vast northern boreal forest of Canada. Climax forests of the taiga are dominated by three coniferous tree species: white spruce on well-drained sites, black spruce on sites underlain by permafrost, and, east of the Cordillera, balsam fir (Viereck and Little 1972, Hosie 1973). Trees are relatively short and have crowns that can extend to the ground. Because none of the three tree dominants is thick-barked, climax vegetation in the taiga has little resistance to fire, which is almost always stand-replacing. These trees also are prone to insect outbreaks, which can defoliate large areas. Because of the homogeneous moisture conditions and topography, and because of even-aged stands created by stand-replacing fires, large areas become flammable simultaneously and, when ignition occurs, fires tend to burn until the weather changes (Johnson 1992). In Alaska during the period 1893-1937, over 2.4 million ha of forest were reported burned by just 19 individual fires (Barney 1971), a mean of 128,000 ha per fire. In the taiga, therefore, snow characteristics, disturbance regimes, and resulting vegetation conditions are homogeneous over large areas.

In the Rocky Mountain West, by contrast, site conditions and forest types vary at small scales. Traveling 10 km from plains to mountaintop, one encounters habitats from dry desert or steppe, through montane and subalpine forests, to tundra, rock, and permanent snow. Across this gradient, natural fire-return intervals can vary from less than 10 years in drier types to over 400 years in moist subalpine stands (Chapter 3). In such settings, fires often start at low elevation, then slow and die as they ascend mountains into moister types. Although Rocky Mountain forests have experienced some very large fires (Gruell 1985, Turner et al. 1997), most fires are topographically limited and smaller than those in the North. Even when comparing areas with similar fire regimes (i.e., similar fire-return periods, stand replacing fires, and forest age structures fitting the negative exponential model, Chapters 3, 15), fires in the Rocky Mountain West are generally smaller, with more complex shapes, due to more complex topography and a wider range of forest types per unit area. For example, wet concave areas dominated by Engelmann spruce tend to burn with less frequency and intensity than adjacent dry convex ones dominated by lodgepole pine. Likewise, post-fire succession tends to be strongly affected by local topography: north aspects will tend toward different post-disturbance trajectories than south-facing slopes. All of these factors tend to produce more heterogeneity within fires and post-fire seres in Rocky Mountain forests of the contiguous United States than in the taiga. Some subalpine forests in the West are so moist and dissected by areas of rock that fire is virtually excluded.

Relative to lynx-prey relationships, the heterogeneity of Rocky Mountain forests results in higher densities of edges, possibly of ecotones, and the relatively fine-scaled juxtaposition of forests of various ages. (See Chapter 9 for a discussion of the potential importance of edge in lynx–hare relationships.) Few forested areas in the Rocky Mountain West the size of a lynx home range (about 75 km^2) contain homogeneous vegetation. Rather, such areas tend to feature many stands comprised of several tree and shrub species having a wide range of stem densities and ages. In contrast, a large burn in the taiga could easily homogenize a landscape as large as several lynx home ranges.

The frequency and kinds of disturbance in forested systems generally vary more strongly along east-west than north-south gradients. This is true at both continental and smaller scales: the eastern Cascades are more fire-prone than the western Cascades, and conifer forests of Montana are more fire-prone than those in New England (Chapter 3). By contrast, disturbance events, including fire and avalanches, occur at the northern and southern edges of the distribution of lynx with remarkably similar frequencies (Chapter 3). In the northeastern United States, broad-scale natural disturbance appears to have been infrequent and most forests would have been in climax condition at the time of European contact (Lorimer 1977). However, today those patterns are virtually irrelevant; the disturbance dynamics of these forests are driven mostly by humans, and forests are much younger. In many places this has resulted in a reduced conifer component, so that what were mixed deciduous-coniferous forests 300 years ago are deciduous forests today. The replacement of mixed stands with pure deciduous stands been accelerated in recent years in the Great Lakes States by the increasing importance of aspen as a crop tree (Chapter 3).

Forest Successional Pathways

In boreal forests, succession generally progresses from herbs and cryptogams soon after disturbance to shrubs, seedlings, saplings, mature trees, and finally to climax forest (Kelsall et al. 1977, Kimmins 1987; Chapter 3). Commonly, after a stand-replacing disturbance, the initial cohort of trees is densely stocked, resulting in self-thinning and low levels of light at the forest floor. Gradually, closed canopies give way to gaps as insect infestation, disease and windthrow kill individual and small groups of trees, allowing light to reach the forest floor. Light gaps encourage shade-intolerant trees, shrubs, and herbs, greatly increasing understory diversity (Pickett and White 1985, Spies et al. 1990, Valverde and Silvertown 1997). However, details of successional pathways will vary according to the nature of local disturbance regimes, tree species composition, and position along major ecological gradients.

Within the taiga, regenerating seres exhibit high stem densities for trees and shrubs for 20-35 years (Foote 1983). The young tree stage that follows features dense deciduous trees with an understory of low shrubs for another 25 years (30-55 years post-fire). This is followed by a conifer-hardwood stage that also maintains an understory shrub component, followed by the climax spruce stage, around 90-150 years post-fire. At this climax stage, understory vegetation is reduced to cryptogams, a few shrubs, and low tree branches. Successional sequences in the taiga, therefore, support understory shrubs and small trees for a long time, perhaps over 60 years. Although understory shrubs mostly disappear in climax spruce forests (Foote 1983), gaps will allow some trees and shrubs to grow, providing some low cover.

In northeastern and Great Lakes boreal forests, successional pathways reflect the strong adaptations of deciduous trees. Hardwoods may dominate entire seral sequences, including climax communities on warm, mesic sites. Here, insects and wind, rather than fire, play important roles in disturbance (Baskerville 1975, Lorimer 1977, Pastor and Mladenoff 1992). Cooler sites, or sites at the extremes of the moisture gradient, follow successional pathways similar to spruce in taiga forests (Dammon 1964, Larsen 1980). The shrub stage often is dominated by dense jack pine and quaking aspen for 5-15 years post-disturbance. After reaching the young tree stage, aspen and pine develop understories of shade-tolerant spruce, fir, maple, and birch until about 40 years post-disturbance. The multistoried climax spruce-fir-mixed hardwood stage is not reached until about 165 years after disturbance (Chapter 3). So, in cooler sites, understory cover will be dense during early shrub stages (5-20 years post-disturbance), then decline and emerge again about 40 years post-disturbance, as climax species grow through the understory. Understory cover then declines again as climax species reach overstory proportions. In hardwood-dominated climax forests, understory cover may be sparse away from canopy gaps, whereas in conifer-dominated climax forests, understory cover tends to be more abundant.

Successional pathways in western montane boreal forests vary dramatically along gradients of moisture and soil nutrients. Climate during the growing season, an important determinant of vegetation, is remarkably similar across the lodgepole pine zone of western forests (Lotan and Perry 1983, table 2). Although total precipitation decreases from west to east across the western contiguous United States, the proportion that falls during the growing season increases so that lodgepole pine forests in Colorado receive about as much summer precipitation as those in the Cascades, which are generally considered more mesic (Lotan and Perry 1983). Of course, sites farther south receive higher incident radiation during the growing season and occur higher on mountains where lower atmospheric pressure causes faster evaporation than near sea level (Knight 1994). Boreal forests with equivalent precipitation will therefore become more xeric farther south.

Soil moisture during the growing season strongly influences shrub and seedling abundance in western coniferous forests. Alexander et al. (1986) described the poor regeneration of lodgepole pine in the Medicine Bow Mountains of southern Wyoming following disturbance on dry sites. However, on some sites, lodgepole pine formed dog-hair stands that persisted for hundreds of years (Alexander et al. 1986:10). In eastern Washington and western Montana, the shrub and young tree stages are distinct but brief (about 5-30 years post-fire), and shrub stem densities are low (Stickney 1981, 1986; Zamora 1982) compared with the taiga (Foote 1983). This pattern becomes more pronounced farther south and east (Colorado and Wyoming), where early seral lodgepole pine tends not to develop a shrub component and tree stem densities can be very low, depending on cone serotiny, fire intensity, elevation, and soils (Alexander et al. 1986).

In subalpine fir climax types in the Pacific Northwest, sapling densities through time are often bimodal (Fig. 14.1, Agee 1993) with peaks occurring in the shrub-sapling stage and again after canopy gaps develop (Spies et al.

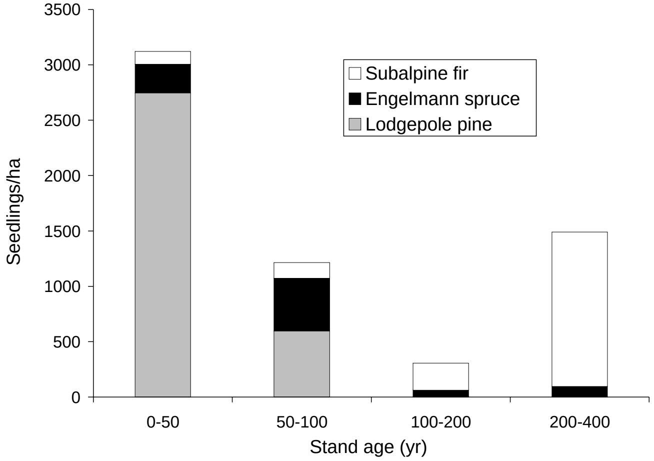

Figure 1—Densities (no./ha) of conifer seedling (< 4 cm dbh) stems in relation to stand age after fire in the Pasayten Wilderness, Washington. Data are from Fahnestock (1976).

1990). Spies and Franklin (1989) reported mean densities of shade-tolerant saplings in moist Douglas-fir forests of Oregon and Washington consistent with this bimodal pattern: 228/ha in young stands, 84/ha in mature stands, and 335/ha in old growth. For understory cover of deciduous shrubs, they reported increasing densities as succession progressed: 6.8% in young stands, 8.9% in mature stands, and 12% in old growth. This bimodal pattern is probably the norm on moist sites. After disturbance, the site will be fully revegetated with deciduous or coniferous tree species and tall deciduous brush. Because moist sites support high leaf areas (Gholz 1982), overstory canopies will be dense, leading to a relative lack of vegetation under the mature canopy and, when the stand is old enough that mortality in the overstory is significant, forest gaps are rapidly colonized. These patterns, however, are far less general on dry sites. On dry sites, tree regeneration after disturbance is extremely variable (Arno et al 1985, Alexander et al. 1986), and these sites often lack tall brush components. As a result, open areas are colonized by grasses or short brush species. Despain (1990), for example, illustrates the small amount of shrub and small tree understory in all but the moistest conifer forest sequences in Yellowstone National Park.

Patterns of Snowshoe Hare and Red Squirrel Abundance

Understanding the successional correlates of wildlife abundance is particularly relevant because many species can be linked to specific seres via forest structure and composition. Forest management alters successional sequences, either by reducing disturbance (fire suppression) or increasing it (timber harvest). However, successional pathways vary greatly in rate, species composition, and physical structure (Pfister et al. 1977, Steele et al. 1981, Moir and Ludwig 1979). Therefore, understanding habitat associations of lynx and their prey must be framed in terms of specific, regional successional trajectories.

Wherever they have been studied, hare densities are positively correlated with densities of small-diameter woody stems (Brock 1975, Wolfe et al. 1982, Pearson 1999, Chapters 6, 7). Density appears to be more important than composition largely because hares consume a wide variety of plant species (Chapter 7). Thus, in general, dense small-diameter stems simultaneously provide both food and cover. Based on these understandings, and lacking site-specific hare density data, we hypothesize that hare densities can be inferred from sapling and tall shrub densities for those forest types known to support hares. In mesic forests, therefore, we argue that hare densities should be bimodal with stand age: highest in early seral conditions, minimal in closed-canopy mature forests, and reaching moderate densities in extremely old gap-phase forests. We do not, however, expect this pattern to be common on dry sites where erratic regeneration and the lack of tall deciduous brush often lead to very open conditions for extensive periods after disturbance. In these stands, hare habitat will only be produced in later seres.

This bimodal association between brushy vegetation and population density has been shown in northwestern California for the shrub-associated dusky-footed woodrat, an important prey of the northern spotted owl. This species is most abundant in dense understory following disturbance, absent from mature forest with scarce shrubs and young trees, and intermediate in abundance in old growth, where increased understory cover accompanies gap succession (Sakai and Noon 1993). Data for snowshoe hares along entire successional sequences are scanty; hares tend to be rare immediately after disturbance, abundant in the shrub-sapling stage, and uncommon in closed-canopy forest (Litvaitis et al. 1985; Koehler 1990a,b; Ferron et al. 1998; Chapters 6,7). In Ontario, Thompson et al. (1989) counted hare tracks on 2 km transects for 5 years. The transects intersected logged stands ≤30 years old and uncut forest 150-200 years old. Average track counts were highest in

20-year-old stands, and abundant and approximately equal numbers of tracks were located in 30-year-old stands and areas of uncut forests. Thompson et al. (1989) attributed the relatively high levels of hare tracks in the old forests to the presence of brush in canopy gaps. Mills and Henderson (unpubl. data) found hares relatively abundant in old-growth forest in northwestern Montana, and Beauvais (1997) found track densities of hares to be positively correlated with variables indicative of late-seral stages in northern Wyoming. Powell (1991 unpubl. data cited in Powell and Zielinski 1994) described a bimodal distribution of snowshoe hare abundance along a successional sequence on the Olympic Peninsula of Washington. These pieces of evidence, while weak, suggest that hares may be relatively abundant in climax conifer forests of the western contiguous United States, and bimodally distributed along successional gradients on mesic sites.

However, in the drier areas within lynx range, including areas in the southern Rocky Mountains of Colorado where regenerating stands develop no shrub stage, suitable hare habitat may only occur in old-growth forests and riparian areas (Lawrence 1955, Dolbeer and Clark 1975). In these areas, snowshoe hare abundance may follow a unimodal distribution that peaks under old-growth conditions with the development of canopy gaps. Two years of snow tracking in a range of stands from young to old growth in northern Wyoming (Beauvais 1997) showed that snowshoe hare tracks were negatively correlated with indices typical of highly fragmented landscapes, such as density of clearcut edge, and positively correlated with indices such as percent of forest cover and percent of spruce-fir cover. Snowshoe hares were also positively correlated with maximum diameters of trees, and with total number of stems within 5 m of sampling points.

Although it is generally acknowledged that early seral stages resulting in dense understory cover provide important habitat for snowshoe hares (Chapters 6, 7), little research has examined the relative importance of gap succession in climax forests for hare habitat. However, the process of gap development, which produces the habitat conditions associated with hares, varies among regions. For instance, gap succession in the Pacific Northwest is driven primarily by single tree mortality, which results in smaller gaps that compose a smaller proportion of the overall forest (Spies et al. 1990). In contrast, in eastern North America wind and insects play larger roles, thereby generating more group-tree mortality, which results in larger gaps and affects a larger proportion of the forest (Kneeshaw and Bergeron 1998). These processes may affect the spatial scales of usable habitat for snowshoe hares within climax or old-growth forests in different regions of North America.

Understanding red squirrel abundances in the context of succession is also important given the role of squirrels as alternative prey for lynx (O'Donoghue et al. 1998b, Chapters 9, 13). Because squirrels eat primarily conifer seeds, in the West their abundance over successional time is linked to cone-producing ages, usually mature (Smith 1970, Obbard 1987) or older (Kemp and Keith 1970, Rusch and Reeder 1978), conifers. Thus, late-successional forest provides habitat within which two prey species important to lynx occur sympatrically and are relatively abundant.

Predator-Prey Communities

The North American distributions of lynx and their two most important prey, snowshoe hares and red squirrels, roughly coincide (Hall 1981). Other potential prey species occupy much smaller geographic ranges, so the availability of alternative prey varies regionally for lynx. In the taiga, these include mice and voles, northern flying squirrels, arctic ground squirrels, beavers, muskrats, grouse and ptarmigan, and a variety of ungulates (Chapter 9). Arctic hares and Alaska hares are tundra dwellers that penetrate forest edges slightly (Hall 1981) and may be eaten in a few areas. In southern boreal forests, however, potential prey communities differ substantially. Medium-sized birds (grouse and ptarmigan), small mammals, and ungulates are relatively abundant throughout the range of lynx, but medium-sized mammal assemblages in southern boreal forests contain many more species than those in the taiga. In montane Colorado, for example, there are four species of leporids: snowshoe hare, white-tailed jackrabbit, mountain cottontail, and desert cottontail (Hall 1981). The coyote, a generalized leporid predator, exploits only snowshoe hares in the North but can switch among various leporids, even those not sympatric in distribution, in southern regions. Although prey-switching by coyotes may seem to ease the competitive pressure on lynx in the southern part of its range, it probably does the opposite. It allows coyotes to switch among leporid species, including snowshoe hares, as seasons, weather, and prey populations change. There is no evidence to suggest that lynx are effective at this kind of prey switching. The greater dietary options available to coyotes in the southern part of the range of lynx may provide a buffer to coyote populations during population lows of hares that is not readily available to lynx and may make coyotes more effective competitors with lynx through time.

Similarly, southern boreal forests during the snow-free season feature diverse medium-sized rodents not present in the taiga, including woodrats, marmots, ground squirrels, fox and eastern gray squirrels, and chipmunks. Although available evidence indicates that snowshoe hares and red squirrels are the most important lynx foods during winter in all portions of their range (Chapters 9, 13), summer diets have scarcely been studied. The influence of this diverse array of alternative prey in the southern portion of the range of lynx is largely unknown.

Lynx also have more potential competitors in the southern part of their range than in the North. In the North, the interference competitors that are likely to be dominant are the wolf and coyote, but coyotes are largely restricted to areas without wolves (Buskirk 1999). In southern boreal forests, by contrast, potential interference competitors of lynx include the coyote, cougar, and bobcat. Data from Montana show that cougars kill lynx and may be a substantial source of mortality (Chapter 13). In the taiga, however, cougars are absent or rare. Coyotes, cougars, and bobcats have expanded their ranges and increased their populations in the contiguous United States within the last 20 years (Chapter 4). Therefore, regional and temporal variation in carnivore communities may contribute to the differential success of lynx populations across North America.

In a few areas of the contiguous United States, wolves are increasing in distribution and numbers, while coyotes are decreasing in response (Crabtree and Sheldon 1999). Lynx should be better able to co-exist with wolves than coyotes, because wolves prey more on ungulates than leporids and are probably too large to be effective interference competitors with lynx (Chapter 4). Accordingly, community conditions for lynx in the Greater Yellowstone Area, where wolf populations are expanding and coyote populations contracting, should improve in coming years.

Broad regional variation in forested landscapes, especially the extent and connectivity of mesic forest types, may mediate competitive interactions involving lynx. Because suitable habitat areas are generally smaller in the southern part of the range, competitors, including those not highly adapted to snow, may be better able to occupy lynx habitat than those in the North (Chapter 4). This process may also be facilitated by human activities, which produce dense systems of roads and trails that probably enable coyotes and other predators to gain access to areas with soft, deep snow (Chapter 4). In general, intensive forest management and concomitant fragmentation of habitat via timber harvesting and road systems are more prevalent in southern boreal forests compared to the taiga. Thus, human-mediated increases in potential competitors and predators may present a more serious threat to lynx populations in southern boreal forests than in the taiga.

Conclusions

Across the vast geographic area occupied by lynx in North America, we observe strong gradients in climate, topography, elevation, soil conditions, snow conditions, plant dominants, disturbance regimes, and successional trajectories. On top of these are added the highly variable influences of humans. Extrapolating information gathered in one part of this region to others must be done with the greatest of care and would be facilitated by additional research. The likelihood of important among-population differences increases with geographical and ecological distances between populations (Chapter 5). This chapter identifies some potentially important ecological differences over the range of lynx and suggests that variation among populations is a key issue for lynx conservation in the contiguous United States.

In the southern range of lynx, the communities of both competitors and prey are more diverse than those in the North. Not only are lynx in the South subject to a different suite of interference competitors, including mountain lions, but exploitation competition with generalists such as coyotes will likely be more significant due to the ability of these predators to prey-switch. The interactions between lynx and competitors in the south is unstudied and represents a major research need.

We question the generalization that the best way to provide habitat for lynx prey, including hares, is to create early-successional forest. On mesic sites, the highest hare densities are generally found in sapling-stage forests after disturbance, but squirrels are absent from these sites. We believe the data, though sparse, also suggest that old gap-phase forests provide a combination of high numbers of squirrels and moderate densites of hares on many sites. Additionally, site moisture appears to be an important correlate of shrub and sapling densities in the early stages following disturbance and, in dry areas of the West where post-disturbance regeneration is erratic, gap-phase old-growth forests may provide relatively higher densities of small-diameter woody stems compared to earlier stages of succession on the same sites.

In areas where boreal forests are highly fragmented, older forests may be an important stabilizing element. Because small areas of boreal forest can be highly altered by single disturbance events, such as fire, hare dynamics associated with post-disturbance conditions will be transient. Older forests are temporally stable, will produce hares in lower but more reliable numbers, and provide squirrels as alternative prey. On dry sites, where young forests do not reliably produce hare habitat, older forests may provide a critical source of hare habitat.

We are cautious in reaching these conclusions because data are so limited. However, the relationship between forest succession and prey abundance is an area of utmost importance to southern lynx conservation. We believe that a well-designed, geographically extensive study to further examine these relationships should be given the highest priority for research. Failure to carefully consider successional trajectories and their structural habitat correlates on a regional and site-specific basis can produce the opposite of intended results, especially with regard to the habitat needs of snowshoe hares. Ultimately, lynx management must take into account unique regional attributes and site conditions relative to disturbance regimes and successional pathways that follow natural disturbance and management events.

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