

Chapter 4

Lynx

Gary M. Koehler, 6505 Markel Road, Deming, Washington

Keith B. Aubry, USDA Forest Service,
Pacific Northwest Research Station, Olympia, Washington

INTRODUCTION

Natural History

Three species of wild cats (felids) occur in the temperate forests of North America: the cougar (*Felis concolor*), bobcat (*Lynx rufus*), and lynx (*Lynx canadensis*). The cougar is found in both temperate and tropical forests from the mountains of southern British Columbia to the southern tip of South America, whereas the bobcat and lynx are restricted to the temperate zone of North America. Bobcats are common throughout a variety of habitats in the conterminous United States, southernmost Canada, and northern Mexico. The lynx, in contrast, occurs primarily in the boreal forests of Alaska and Canada, but its range extends south into the northern portions of the western mountains, where environmental conditions at high elevations support boreal forest habitats similar to those found in northern regions.

The bobcat and lynx are both short-tailed cats, but the bobcat is smaller than the lynx and has relatively shorter legs and smaller paws. The lynx's short tail is completely tipped with black, whereas the bobcat's tail is generally longer and is barred with black only on the upper surface (Nowak and Paradiso 1983). The bobcat looks much like a house cat (*Felis catus*) in body form but is about two or three times larger. The lynx differs in body proportions, however, having relatively long legs and hind legs that are longer than the forelegs, giving it a stooped appearance (Quinn and Parker 1987).

The winter pelage of the lynx is dense and has a grizzled appearance with grayish-brown mixed with buff or pale brown fur on the back, and grayish-white or buff-white fur on the belly, legs, and feet. Its summer pelage is more reddish to gray-brown. Male lynx are slightly larger than females, with total length averaging 85 cm compared to 82 cm, and weight av-

eraging 10 kg for males and 8.5 kg for females (Quinn and Parker 1987). Both sexes have prominent ear tufts and a flared facial ruff. The paws of the lynx have twice the surface area of those of the bobcat (Quinn and Parker 1987). The lynx's long legs and broad paws enable it to negotiate the deep snows of the boreal forests and effectively hunt its principal prey, the snowshoe hare (*Lepus americanus*). The bobcat, lacking these features, is largely restricted to habitats where deep snows do not accumulate (Koehler and Hornocker 1991). Despite physiological and behavioral differences that may permit lynx and bobcats to exploit different niches (Parker et al. 1983), lynx apparently do not compete well with bobcats (Parker et al. 1983; Turbak 1991). Thus, habitat alterations that favor a northward range expansion by bobcats may not bode well for lynx, particularly in suboptimal habitats.

The distribution and abundance of the lynx appears to be tied to that of the snowshoe hare. Both species are confined to northern forest environments (Hall 1981). Hares seek dense conifer thickets to feed on woody seedlings and saplings and to escape predators and extreme cold; lynx frequent these habitats in search of prey. When foraging, lynx select forested habitats where hares are plentiful and use this cover to stalk or wait for hares to appear. From the forested peninsulas of western Alaska to the eastern islands of Canada and in the mountains of the western United States, hares comprise 35-97% of the lynx diet (table 1). Although snowshoe hares are the primary food for lynx throughout its range, they also feed on mice, squirrels, grouse, and ptarmigan, especially during the summer months (McCord and Cardoza 1982).

Hares not only determine where lynx are found but also influence how many lynx may occupy an area. This is dramatically illustrated in Alaska and central Canada, where hare populations cycle in abundance at varying amplitudes, with population

Table 1.--Percent occurrence of prey items in the winter diet of lynx determined from analysis of scats (ST) or digestive tracts (DT). Sample size in parentheses.

Season, location	Percent of sample				
	Hares	Tree squirrels	Mice	Ungulates	Grouse
Winter diets					
Alaska ¹					
(ST= 161)	64	10	9	5	7
Alberta ²					
(DT = 879)	35-90	9-12	4-28	22-3	2-6
(ST = 260)	61	5	10	3	4
Alberta & NWT ³					
(DT = 52)	79	2	10	6	10
Newfoundland ⁴					
(ST,DT = 152)	85	-	5	>13	-
Nova Scotia ⁵					
(DT = 75)	97	1	3	5	3
(ST = 55)	93	-	7	5	4
Summer diets					
Alaska ¹					
(ST = 42)	38	28	15	-	7
Alberta ²					
(ST = 38)	71	2	87	5	5
Alberta & NWT ³					
(DT = 23)	52	9	22	-	-
Newfoundland ⁴					
(ST,DT = 92)	65	-	30	>3	-
Nova Scotia ⁵					
(ST = 441)	70	4	4	9	1
Annual diets					
Washington ⁶					
(ST = 29)	79	24	-	3	3

¹ Staples and Bailey 1993, unpubl.

² Brand and Keith 1979, Brand et al. 1976.

³ van Zyll de Jong 1966.

⁴ Sounders 1963o.

⁵ Parker et al. 1983.

⁶ Koehler 1990.

densities changing 2-200 fold within a 5-year period. As this phenomenon is repeated, periods of hare scarcity occur approximately every 10 years (Brand and Keith 1979). In areas where snowshoe hare populations exhibit this cycle, lynx also undergo dramatic population fluctuations. As part of a predator-prey oscillation, lynx populations lag several years behind hares, going from near extinction to densities of 10 to 20 lynx/100 km² during their population peaks (Bailey et al. 1986; Brand and Keith 1979; Parker et al. 1983). At the southern limits of its distribution, however, snowshoe hare populations do not undergo dramatic cycles due apparently to the presence of predators and competitors that do not occur in northern regions and to the patchiness of suitable habitat

(Dolbeer and Clark 1975; Wolff 1980, 1982). Consequently, lynx populations appear also not to cycle in abundance at southern latitudes (Koehler 1990). In general, lynx and snowshoe hares in the western mountains of the United States exhibit life history characteristics similar to those occurring during hare population lows in the northern boreal forests (Brittall et al. 1989, unpubl.; Koehler 1990; Dolbeer and Clark 1975; Wolff 1980, 1982). This difference in the population dynamics of lynx and snowshoe hares in the southern portions of their ranges has strong implications for the management and conservation of lynx in the western mountains.

Several excellent literature reviews have recently been produced that describe lynx and snowshoe hare

biology in northern areas where populations are cyclic (Butts 1992, unpubl.; Washington Dept. of Wildlife 1993, unpubl.; Weaver 1993, unpubl.). The emphasis of this chapter, however, will be on the population dynamics and habitat relationships of lynx in either the western mountains or in northern boreal forests during times of low hare densities. This information provides the most meaningful conceptual framework for management and conservation of lynx in the western mountains.

During periods of hare and lynx abundance in northern regions, when competition for prey is keen and available territories are occupied or, during periods of prey scarcity after hare numbers have crashed, lynx may undergo dramatic movements in search of adequate prey (Poole 1993, unpubl.). During these times, lynx have been known to travel as far as 1,100 km (Mech 1980; Poole 1993, unpubl.; Slough and Mowat 1993, unpubl.) and are found in atypical habitats, such as agricultural areas or geographic areas far south of their normal range (Mech 1980). Although speculative, this process may be important for the persistence of lynx populations in marginally suitable habitats at the periphery of their range. In addition, these extensive movements presumably facilitate gene flow among populations, which may explain why the lynx appears to be genetically homogeneous throughout its range; all lynx populations, with the exception of those occurring in insular Newfoundland, are classified as a single subspecies (Hall 1981).

Current Management Status

As with most felids of the world, except for those that are classified as threatened or endangered with extinction, the lynx is listed on Appendix II of the Convention on International Trade of Endangered Species. This listing requires the exporting country to provide evidence that trade will not threaten or endanger the species and that items of trade, such as pelts, be regulated and monitored.

Lynx populations in Alaska and most of Canada are generally considered stable (table 2), although few reliable population estimates have been made (Anonymous 1986, unpubl.; Quinn and Parker 1987). Large populations are found in southern Quebec, northern British Columbia, Yukon, and Northwest Territories (IUCN, in press). In Canada, lynx are considered endangered only in New Brunswick; however, they are believed to have been extirpated from

Table 2.-Current management status of lynx in states and provinces of North America and lands of federal jurisdiction within the United States (Anonymous 1986, unpubl.; Butts 1992, unpubl.; IUCN, in press; Washington Dept. of Wildlife 1993, unpubl.).

Jurisdiction	Status or classification	Seasons or regulations
Alaska	Furbearer Fur animal	Hunting or trapping permit required, harvest limit 2, season 1 to 4.5 months,
Colorado	Endangered	
Idaho	Furbearer	Quota 3, December season, hunting or trapping permit required.
Maine	Protected	
Michigan	Protected	
Minnesota	Furbearer	Closed season since 1984.
Montana	Furbearer	Quota of 2, Season 1 Dec-15 Feb.
New Hampshire	Protected	
New York	Protected	
North Dakota	Furbearer	Closed season since 1981.
Oregon	Game Species	Closed season.
South Dakota	Nongame Monitor Species	
Utah	Threatened	
Vermont	Protected	
Washington	Threatened	
Wisconsin	Endangered	
Wyoming	Protected	
Alberta		Harvest seasons.
British Columbia		Harvest seasons.
Northwest Territories		Harvest seasons.
New Brunswick	Endangered	
Newfoundland		Harvest seasons.
Nova Scotia	Extirpated on peninsula	Closed since 1980. Harvest seasons.
Ontario		
Prince Edward Island	Endangered	
Quebec		Harvest seasons.
Saskatchewan		Harvest seasons.
Yukon		Harvest seasons.
USDA Forest Service	Sensitive	Region 1,2,4,6.

Prince Edward Island and mainland Nova Scotia. Lynx are considerably more rare in the conterminous United States. The largest populations in the United States outside of Alaska occur in the northern portions of Washington and Montana.

A petition was submitted to the U.S. Fish and Wildlife Service (USFWS) in August 1991 to list the lynx as endangered in the northern Cascade Range of Washington. In February 1992, the USFWS denied the petition because substantial scientific or comer-

cial evidence was not available indicating that the lynx population in the north Cascades should be listed as endangered (Federal Register 1992). In April 1992, the USFWS agreed to reevaluate its 90-day finding on the petition in light of new information submitted by the petitioners. The USFWS found that there was no substantial new evidence indicating that the requested action was warranted and concluded that the north Cascades lynx population is not listable because it is not isolated from lynx populations elsewhere (Federal Register 1993). The USFWS also found, however, that a status review should be conducted throughout lynx range in the conterminous United States; this review is currently underway.

The lynx was classified as endangered in Colorado in 1973 (Halfpenny and Miller 1980, unpubl.) and Washington listed the lynx as threatened in October 1993 (Washington Dept. of Wildlife 1993, unpubl.). The lynx is protected or is considered to be a species of special concern in Wyoming and Utah, but it is still trapped during a restricted season in Idaho and Montana (table 2). The USDA Forest Service, which administers the majority of lands where lynx occur in the conterminous United States, considers the lynx to be a sensitive species in all Regions containing lynx populations (Regions 1, 2, 4, and 6; see Appendix C). This designation refers to species for which population viability is of concern as evidenced by significant current or predicted downward trends in population numbers, population density, or habitat capability.

Lynx are relatively common throughout forested areas of Alaska and most of Canada, although intensive trapping in the past has eliminated or temporarily reduced numbers in localized areas within that region (Bailey et al. 1986; Todd 1985). The conservation of lynx populations is of greatest concern in the western mountains of the conterminous United States at the southern periphery of the species' range. Because recruitment is low in this region and many lynx populations, especially those in Utah, Wyoming, and Colorado, are geographically isolated, trapping and forest management activities may pose significant threats to the persistence of these populations.

DISTRIBUTION, TAXONOMY, AND ZOOGEOGRAPHY

Distribution in North America

Lynx occupy regions in North America of arctic or boreal influence. They are restricted to forested habi-

tats within this region and are found from western Alaska to the eastern edge of Newfoundland. The northern boundary of this range coincides with the northern extension of the boreal forests; lynx are absent north of the Ungava Peninsula in Quebec and in the northern regions of the Northwest Territories (Anonymous 1986, unpubl.). The lynx's historic range also included the northern portions of the conterminous United States in the Cascade Range of Washington and Oregon, south in the Rocky Mountains to Utah and Colorado, and east along the Canadian border to the Lake States (McCord and Cardoza 1982; Quinn and Parker 1987).

Except for the southern boundary of its range, the distribution of lynx in North America probably has not changed much during historical times (Quinn and Parker 1987). Destruction of forests for timber and incursions of agriculture and settlements, however, may have displaced lynx occurring in the Lake States (Jackson 1961) and southern regions of Manitoba to Alberta (Anonymous 1986, unpubl.; Quinn and Parker 1987). Lynx have probably been extirpated from Prince Edward Island and the mainland of Nova Scotia (Anonymous 1986, unpubl.), and their range appears to have retracted on Cape Breton Island after the introduction of bobcats (Parker et al. 1983).

Taxonomy

The taxonomic status of the lynx is an issue of controversy among authorities. The debate concerns both the generic status of lynx throughout the world and the specific status of lynx in North America. It is unclear whether lynx throughout the world should be classified within a separate genus *Lynx*, or whether they should be placed within the more inclusive genus *Felis*. In either case, there is also confusion about whether the Canadian lynx should be considered a separate species from the Eurasian lynx. Thus, some authorities (McCord and Cardoza 1982; Tumlinson 1987) consider the Canadian lynx to belong to the Holarctic species *Felis lynx*. Others (Jones et al. 1992) agree that lynx represent a Holarctic species but consider lynx to be generically distinct from other cats and place the Canadian lynx within the species *Lynx lynx*. Others (Hall 1981; Wozencraft 1989, 1993), however, believe that Eurasian and Canadian lynx represent distinct species and place the Canadian lynx in the species *Lynx canadensis*.

Lynx and bobcat are believed to have evolved from Eurasian lynx that immigrated to North America

from Asia via the Bering land bridge during the Pleistocene (Quinn and Parker 1987; Tumlinson 1987). It is speculated that the bobcat and the Canadian lynx represent the descendants of two separate colonizations of North America by the Eurasian lynx. The first immigrants became established in the southern portions of the continent about 20,000 years ago, when glaciers covered the northern regions. These populations, that were isolated in ice-free areas in the southern portions of the continent, evolved into the bobcat. Some time later, the North American continent was invaded by Eurasian lynx a second time. These populations established themselves in northern boreal forests in areas that were occupied previously by glaciers, and evolved into the Canadian lynx (Quinn and Parker 1987).

Zoogeography of Lynx in the Western Mountains

The boreal forests of Canada and Alaska are the primary habitat of lynx in North America. Populations occurring in the western mountains of the conterminous United States occupy peninsular extensions of this distribution. Lynx distribution at southern latitudes represents the occupation of marginally suitable habitat that decreases in quality and availability as one moves southward. Ecoprovinces where lynx populations occur in the western mountains include the Thompson-Okanogan Highlands of northeastern Washington, the Shining Mountains of northern Idaho and northwestern Montana, the Northern Rocky Mountain Forest of southwestern Montana and northwestern Wyoming, and the Colorado Rocky Mountains of west-central Colorado (see Appendices A and B). A brief review of the historical zoogeography and current population status and ecology of lynx and snowshoe hares in the western mountains will illustrate the marginal nature of boreal habitats in that region.

Lynx have apparently never occupied the Sierra Nevada of California in historic times (Grinnell et al. 1937; Ingles 1965). Although the lynx has been found in Oregon, historical records indicate that it has always been rare; only a few specimen records are known from high elevations of the Cascade Range and the Willowa Mountains in the northeast (Bailey 1936). A lynx shot in northeastern Oregon in 1964 was the first record of a lynx being taken in Oregon since 1935 (Coggins 1969). Oregon clearly represents

the southern margin of suitable lynx habitat along the Pacific Coast. Lynx are now considered to be extirpated from the state (Ingles 1965; McCord and Cardoza 1982), although several sightings have been reported recently (Zielinski, pers. comm.). Apparently, populations have always been so low in Oregon that they were unable to persist with the onset of human settlement of that region. The lynx still occurs in Washington, but its range has retracted northward. Taylor and Shaw (1927) reported the lynx to be a component of the fauna occurring in the higher elevations of Mount Rainier National Park in the central Washington Cascades, and Dalquest (1948) showed its range extending south in the Cascades to near the Oregon border on Mount Adams, and in the Blue Mountains in the southeastern corner of the state; there are no historic records of lynx in either the Olympic Mountains or Coast Range of Washington. A current description of lynx distribution in Washington (Washington Dept. of Wildlife 1993, unpubl.) indicates that lynx are now restricted to the northeastern Cascade Range and several isolated areas in the Okanogan Highlands of northeastern Washington. The Okanogan population was studied with radiotelemetry in the 1980's (Brittell et al. 1989, unpubl.; Koehler 1990) and most of the information available on the ecology, population dynamics, and management of lynx in the western mountains of the United States comes from these studies.

This pattern of decreasing habitat suitability with decreasing latitude is also evident in the Rocky Mountains. Lynx populations are also present in northern Idaho and western Montana. Historical records are relatively numerous in the panhandle of Idaho; Davis (1939) reported lynx occurring in the mountainous regions north and east of the Snake River in Idaho, and Rust (1946) claimed that they were fairly well distributed in wooded areas of the northern counties with 25 or 30 lynx being taken annually by trappers and hunters. Historical reports from western Montana also indicate that the lynx was fairly numerous in recent times. Bailey (1918) lists the lynx as being more or less common throughout Glacier National Park, and the Montana Fish and Game reports that from 1959-1967, a total of 990 lynx were taken by trappers statewide (Hoffman et al. 1969). According to Hoffman et al. (1969), lynx are most common in the northwestern areas of the state, and they decrease in abundance south and east. Populations in western Montana are large enough for scientific study; two radiotelemetry studies of

lynx movements in western Montana were conducted in the early 1980's (Brainerd 1985; Smith 1984).

Although early trappers had apparently reported taking lynx from northern Nevada (Bailey 1936), Hall (1946) includes the lynx on a list of hypothetical species for Nevada based on a lack of museum specimens. Further investigation by Schantz (1947), however, revealed the existence of a single specimen of lynx taken from north-central Nevada in 1916. Records of lynx are scarce in Wyoming, Utah, and Colorado. A review of existing records of lynx in Wyoming by Long (1965) shows that 15 museum specimens exist, and all are from the northwestern corner of the state. According to Long (1965) the lynx was "confined to high, inaccessible (to man) ranges of northwestern Wyoming, if not extirpated at the time of this writing." Later authors (Clark and Stromberg 1987; Clark et al. 1989) agree that the lynx remains extremely rare in Wyoming.

Reports by trappers in 1915 and 1916 (Barnes 1927) suggest that lynx were relatively common in Utah at that time; however, Durrant (1952) questions the validity of these reports. He believes that many of these records are actually of bobcats because the feet and tail are often removed from pelts, and also because large bobcats are commonly referred to as lynx cats in the fur trade. Durrant (1952) reports that only two lynx from Utah exist in museum collections, and he is of the opinion that "if *L. c. canadensis* occurs at all in Utah at present, there are only a few animals in the Uinta Mountains" in north-central Utah. Although seven lynx specimens were collected from the Uinta Mountains in Utah from 1957-1972, since that time only sightings and tracks have been reported (McKay 1991, unpubl.).

Nine museum specimens of lynx exist from eight counties in Colorado (Halfpenny and Miller 1980, unpubl.), but it is generally agreed that lynx were never numerous in the state and are presently extremely rare (Lechleitner 1969; Halfpenny and Miller 1980, unpubl.). Four of these specimens were collected from 1969-1972, and all were from a relatively small area in the west-central portion of the state (Halfpenny and Miller 1980, unpubl.). Records from this state represent the southernmost extension of current lynx distribution in North America.

Existing records clearly show that lynx are rare at the southernmost extensions of its range in Wyoming, Utah, and Colorado, both historically and at present, and that any populations that occur in this area are disjunct and isolated in distribution. It seems doubt-

ful, therefore, that gene flow is occurring among these populations. Because boreal habitat is found at higher and higher elevations as one moves southward in the western mountains, suitable habitat for lynx eventually becomes scattered on isolated mountain peaks (Findley and Anderson 1956). Museum records of lynx in Wyoming, Utah, and Colorado overlap precisely with the range of boreal forest habitat depicted by Findley and Anderson (1956). Given the rarity of records and the dispersal capabilities of lynx, it is possible that existing records represent short-term residents or individuals wandering and dispersing, rather than reproductively stable populations; viable lynx populations may never have occurred in historic times in the southern Rocky Mountains. Thus, lynx conservation efforts may best be directed at populations occurring in northeastern Washington, northern Idaho, and western Montana.

Because they are contiguous with lynx populations that undergo periodic dramatic increases in numbers, populations near the Canadian border may have benefitted from periodic incursions of lynx as populations peaked in northern latitudes (Hoffman et al. 1969; Mech 1980; Quinn and Parker 1987). For example, there were dramatic increases in lynx harvests in western Montana and the northern Great Plains in 1962-1963 and 1971-1972 (Adams 1963; Hoffman et al. 1969; Mech 1973). However, after a population irruption of lynx in Minnesota following a cyclic high in Canada in 1972, trappers reported capturing 215 lynx in 1972, 691 in 1973, 88 in 1974, and 0 in 1975 (Mech 1980). Mech (1980) also showed that immigrating lynx occupied very large home ranges, exhibited little reproductive productivity, and were susceptible to human-caused mortality. Thus, immigration of lynx into marginal habitats during population highs in the north may ultimately have little effect on their population persistence at lower latitudes.

Management Considerations

1. Because of the peninsular and disjunct distribution of suitable lynx habitat in the western mountains of the conterminous United States, populations in that region are likely to be of greatest conservation concern.

2. Both historical and recent lynx records are scarce from the western mountains, which makes identifying range reductions and determining the historical distribution of reproductively stable populations in that region difficult, if not impossible.

Research Needs

1. Reliable information on the current distribution and abundance of lynx populations throughout the western United States is urgently needed.

POPULATION ECOLOGY

Population Dynamics of Snowshoe Hares and Lynx in the Western Mountains

The 10-year cycle of dramatic increases in population densities for both snowshoe hares and lynx in the boreal forests of Canada and Alaska is well-known (Keith 1963; Brand and Keith 1979; Brand et al. 1976; Nellis et al. 1972; and others). Although this phenomenon is of critical importance for the conservation and management of lynx populations in northern boreal forests, neither lynx (Brittall et al. 1989, unpubl.; Koehler 1990) nor snowshoe hare (Chitty 1950; Dolbeer and Clark 1975; Wolff 1980; Koehler 1990) populations in the western mountains of the United States exhibit such cycles. It appears, rather, that both species occur in that region at relatively stable densities comparable to those occurring during population lows in the northern boreal forests (Brittall et al. 1989, unpubl.; Koehler 1990; Wolff 1980, 1982).

A compelling hypothesis has recently been proposed by Wolff (1982) to explain this latitudinal variation in the population dynamics of hares and lynx. Wolff speculates that the presence of additional predators and competitors of hares at lower latitudes largely accounts for this pattern. Apparently, during hare population lows in Alaska, hares occupy less than 10% of suitable hare habitat, which appears to be comparable to the normal dispersion of hares in the western mountains. As population density increases in northern regions, hares begin dispersing into suboptimal and marginal habitats. When predator populations have crashed and competitors are few, hares moving into such habitats are able to establish themselves and reproduce, and the population slowly builds again in numbers. In contrast, hares dispersing into low-quality habitat in Colorado suffer increased mortality from predation and are not able to establish themselves in such habitats (Dolbeer and Clark 1975). The reproductive rates of hares in Colorado did not differ significantly from those in northern regions, indicating that limitations in the intrinsic rate of increase do not explain the latitudinal gradient in population cycles (Dolbeer and Clark 1975). Rather, the apparent lack of hare population

cycles in the western mountains is best explained as resulting from the presence of more stable populations of predators, lower-quality suboptimal habitats, and, possibly, from the presence of fewer competitors at southern latitudes. In addition, a regional mosaic of early successional habitats created by frequent large-scale wildfires in northern forest ecosystems may contribute to higher quality lynx and hare habitats in that region (T. Bailey, pers. comm.).

The major predators of hares in the north are the lynx, goshawk (*Accipiter gentilis*), red fox (*Vulpes vulpes*), and great-horned owl (*Bubo virginianus*). In that region, lynx, goshawk, and great-horned owl are obligate, migratory predators that all exhibit a delayed density-dependent cycle with snowshoe hares, resulting in a relaxation of predation pressure after snowshoe hare populations have crashed. In contrast, the major predators of snowshoe hares in the western mountains are the coyote (*Canis latrans*), bobcat, red fox, and several species of hawks and owls. These predators are facultative and resident, and their populations do not cycle in response to hare numbers. The presence of predators at stable densities prevents snowshoe hares from becoming established in suboptimal habitats. Boreal forest habitat in northern regions tends to be relatively continuous in distribution. The insular nature of preferred habitats in the south, however, whereby adjacent habitats can be of very low quality, may hinder the occupation of suboptimal habitats by snowshoe hares. No other species of leporid occupies the northern boreal forests; thus, the presence of potential competitors such as jackrabbits (*Lepus* spp.) and cottontails (*Sylvilagus* spp.) in the western mountains may also limit snowshoe hare populations.

Reproductive Biology

Lynx have a high potential for population growth but, as with other life history parameters, recruitment is influenced by the abundance of its principal prey, the snowshoe hare (Bailey et al. 1986; Brand and Keith 1979; Brand et al. 1976; Nellis et al. 1972; O'Conner 1986; Parker et al. 1983; Slough and Mowat 1993, unpubl.). Recruitment is high during periods of hare abundance primarily because of increased kitten survival. However, periods of high hare numbers are also accompanied by increased reproductive rates for yearlings and increased litter sizes among females in all age classes (Brand and Keith 1979; Brand et al. 1976; O'Conner 1986; Parker et al. 1983).

From examination of necropsied carcasses from Alaska, O'Conner (1986) found lynx to ovulate from late March to early April and give birth in late May after a gestation period of 60-65 days. This breeding schedule has also been reported for Ontario (Quinn and Thompson 1987), Alberta (Nellis et al. 1972) and Newfoundland (Saunders 1964). Kittens observed in north-central Washington in early July (Koehler 1990, unpubl. data) appeared to have been born in late May or early June, suggesting that conception occurs in March and April at southern latitudes as well. In Alaska, the mean number of corpora lutea and placental scars, the age of first breeding, the proportion of females breeding, the proportion of kittens breeding, and the percentage of juveniles present in the population all reached highest levels the first spring after hare numbers peaked (O'Conner 1986). This time lag may differ in other regions depending on the density of predators other than lynx, weather factors, and availability of alternate prey (O'Conner 1986).

Brand et al. (1976) found that females were capable of becoming pregnant at 10 months of age under optimal conditions, based on the presence of corpora lutea, but Parker et al. (1983) concluded that most females reach reproductive maturity at 22 months. Age of first ovulation can be influenced by hare abundance, however; 61-99% of lynx ovulate as kittens during periods of hare abundance compared to only 10-49% as hare numbers decrease (O'Conner 1986, van Zyll de Jong 1963, Brand et al. 1976, Brand and Keith 1979). Quinn and Thompson (1987) found that 96% of yearlings, 99% of 2-year-olds, and 100% of females >3 years old ovulated during a period of hare abundance in Ontario. O'Conner (1986) also demonstrated a difference in ovulation rates between periods of hare scarcity and abundance. During times of hare abundance, counts of corpora lutea averaged 6.2 ± 0.3 (95% CI) to 6.4 ± 1.1 for yearlings (indicating they ovulated as kittens) and 16.5 ± 1.3 to 15.4 ± 2.3 for adults, compared to periods of hare scarcity when counts were 0.5 ± 0.7 for yearlings and 8.6 ± 1.3 for adults.

Counts of placental scars have been used to estimate pregnancy rates and *in utero* litter sizes, although such counts may not accurately reflect actual litter size because some implanted embryos may not survive (Quinn and Thompson 1987). Pregnancy rates range from 33-79% for yearlings and 73-92% for adults during periods of hare abundance, compared to rates of only 0-10% for yearlings and 33-64% for adult females when hares were scarce (Brand

and Keith 1979; O'Conner 1986; Quinn and Thompson 1987). During a period of hare abundance, Quinn and Thompson (1987) found that although 96% of yearlings ovulated, only 33% became pregnant, whereas 80% of 2-year-olds and 92% of females >3 years old became pregnant. Brainerd (1985) examined 20 female carcasses from western Montana and found pregnancy rates of 44.4% for juveniles and 100% for adults. Among lynx that had colonized areas of low prey density in Minnesota, only 1 of 14 live-captured females showed signs of nursing and only 2 of 22 female carcasses examined showed evidence of implantation (Mech 1980). The number of placental scars averaged 3.5-3.9 for yearlings and 4.4-4.8 for adults during periods of hare abundance, which decreased significantly to 0.2 for yearlings and 1.4-3.4 for adults when hares were scarce (Brand and Keith 1979; O'Conner 1986; Parker et al. 1983; Quinn and Thompson 1987). Average litter size (based on placental scars) in western Montana was 2.75, with a range of 1-5; litter size for yearlings was 1.75 and for adults, 3.25 (Brainerd 1985).

During hare population declines, there is increased kitten mortality prior to winter. Brand et al. (1976) found no kittens present on their Alberta study area during a low in hare numbers. Kitten production and survival in north-central Washington during 5 1/2 years of a 7-year period (1980-1983, 1985-1987) was comparable to a 5-year period of low productivity measured at northern latitudes when hares were scarce (Brittall et al. 1989, unpubl.; Koehler 1990; Brand et al. 1976).

In Alberta, recruitment of kittens to the winter population decreased dramatically 2 years after the peak, and was near zero for 3-4 years during periods of hare scarcity (Brand and Keith 1979). No litters were produced during 5 winters when hare densities were lower than 1.4 hares/ha, and mean litter size increased from 1.3-3.5 as hare density increased from 1.8-5 hares/ha (Brand et al. 1976). In north-central Washington where hare numbers were believed to be low, Koehler (1990) found only 1 kitten surviving to the winter from 8 kittens present among 3 litters in July, indicating that kitten mortality is high during the snow-free season. A disparity in the ratio of females with corpora lutea compared to those observed nursing from August to October, and the few kittens present in fall harvest figures, led Nellis et al. (1972) and Parker et al. (1983) to speculate that several factors result in lower reproductive rates during periods of hare scarcity, including preimplantation

losses, intrauterine losses, and mortality of kittens during summer.

Mortality

As with reproductive parameters, mortality is also influenced by the relative abundance of hares. Although data are scarce, natural mortality rates for adult lynx average $\leq 27\%$ per year (Koehler 1990; Slough and Mowat 1993, unpubl.). Bailey et al. (1986) observed no mortality from predation or disease between 1977 and 1984 on their study area in Alaska. In the Yukon, Ward and Krebs (1985) found only 1 of 11 radio-collared animals dying from natural causes. Brand and Keith (1979) calculated natural mortality rates from May to November in Alberta of 34-68% during a snowshoe hare decline. In the Northwest Territories, annual mortality for radio-collared lynx increased from 0.10-0.79 as hares declined (Poole 1993, unpubl.). Although starvation appears to be the most significant cause of natural mortality, predation also occurs (Koehler 1990; Koehler et al. 1979; Poole 1993, unpubl.).

During periods of decreasing hare numbers, mortality rates for kittens may be three times that for adults (Brand and Keith 1979). The cause of postpartum mortality of kittens is most likely related to starvation, as females are more likely to feed themselves first (Brand and Keith 1979). Thus, it appears there may be a minimum density of hares at which females are no longer able to successfully rear kittens (Nellis et al. 1972). Koehler (1990) observed a kitten mortality rate of 88% during summer-fall seasons for 8 kittens from 3 litters in Washington, which is similar to mortality rates of 65-95% for kittens in Alberta during a 3-year period of hare scarcity (Brand and Keith 1979). Mortality for kittens of juvenile females is higher (80-100%) than that for kittens of older females (30-95%), indicating that juveniles contribute little to recruitment (Slough and Mowat 1993, unpubl.).

Trapping can be a significant source of mortality for lynx (Bailey et al 1986; Carbyn and Patriquin 1983; Mech 1980; Nellis et al. 1972; Parker et al. 1983; Ward and Krebs 1985). During a period of high recruitment in Ontario, Quinn and Thompson (1987) estimated overall trap mortality for lynx at 38%. Where exploitation is intense and recruitment is low, trapping can significantly depress lynx populations. In the intensively trapped Kenai National Wildlife Refuge in Alaska, Bailey et al. (1986) found that trapping accounted for 44-86% of annual mortality and estimated that trappers may have removed as much as

80% of the lynx population in their study area. Parker et al. (1983) estimated that trappers removed 65% of their study population in Nova Scotia. Among 14 radio-collared animals in Minnesota, at least 7 were killed by humans (Mech 1980), and all 5 study animals in Manitoba and 8 of 11 in the Yukon were taken by trappers (Carbyn and Patriquin 1983; Ward and Krebs 1985). On the Kenai Peninsula, juveniles were 5 times more vulnerable to trapping than adults, a phenomenon that may be associated with family cohesiveness, since several juvenile siblings can easily be trapped from a small area (Bailey et al. 1986).

Trapping females that are accompanied by kittens often results in the death of those kittens (Bailey et al. 1986; Carbyn and Patriquin 1983; Parker et al. 1983). Bailey et al. (1986) reported that 2 of 3 kittens starved to death after their mothers were trapped. Apparently kittens are unable to obtain sufficient prey by themselves during the winter (Bailey et al. 1986). Yearlings also appear to be dependent upon their mothers for survival. Parker et al. (1983) observed an increase in numbers of yearlings trapped as the harvest season progressed, presumably because more yearlings were orphaned. In addition, kittens of yearling females have higher mortality rates (80-100%) than kittens from adult females (30-95%) (Slough and Mowat 1993, unpubl.).

Emigrating or nomadic lynx can suffer high trapping mortality. In the Yukon, during a period of low hare numbers, Ward and Krebs (1985) reported that all radio-collared lynx that emigrated from their study area were subsequently trapped. Slough and Mowat (1993, unpubl.) found that 10-20% of lynx that emigrated from or that occupied areas peripheral to their untrapped study area were harvested by trappers. Fur harvest returns for lynx also indicate a differential rate of mortality among the sexes, whereby males are more vulnerable than females to trapping mortality (Mech 1980; Parker et al. 1983; Quinn and Thompson 1987), presumably because of their greater mobility and larger home ranges. This pattern has been demonstrated for other furbearers, as well (Buskirk and Lindstedt 1989). Assuming an even sex ratio at birth, Quinn and Thompson (1987) showed from fur harvest records that the annual rate of trap mortality for males was 0.46 ± 0.26 (90% CI) compared to 0.28 ± 0.17 for females, and that increased male vulnerability begins at the age of 1.5 years. Bailey et al. (1986) also found males to be twice as vulnerable to trap mortality as females.

Trapping mortality appears to be additive, since most natural mortality occurs during summer

months prior to the winter trapping season. In their Alberta study area, where lynx trapping did not occur, Brand and Keith (1979) observed no change in the population over the winter, although populations declined elsewhere where trapping occurred. The importance of trapping as a source of mortality is correlated to the price of lynx furs (Todd 1985). Brand and Keith (1979) estimated that only 10% of the fall population was trapped when pelt prices averaged \$44/pelt, whereas 17-29% were trapped when prices increased to \$101 /pelt.

Age and Sex Structure

Fur harvest data can provide an indication of the direction and amplitude of population changes (O'Conner 1986), although caution must be applied when using these data to interpret population parameters. For example, Brand and Keith (1979) found only a 4.3-fold increase in lynx numbers on their Alberta study area when harvest data for the Province indicated a 20-fold increase. Caution should also be applied when using harvest statistics to estimate population sex ratios. In Ontario, 58% of trapped lynx were males (Quinn and Thompson 1987), whereas in Alberta, 71% were males (Brand and Keith 1979).

As the density of hares declines, the proportion of kittens in harvest samples decreases. O'Conner (1986) examined trapper-killed carcasses and found that during periods of hare abundance in 1963-1964 (N=745) and 1970-1971 (N=114), 40% and 32% of lynx trapped were kittens and 40% and 55% were yearlings, respectively. Harvest percentages dropped to 0-3% for kittens and 8-17% for yearlings, however, when hare numbers were low. In Alberta, as hare numbers dropped, the proportion of kittens went from 31-7% (Brand and Keith 1979), and Parker et al. (1983) documented a decline from 29-2% for kittens and 52-39% for yearlings during a hare decline in Nova Scotia.

Brand and Keith (1979) found only 1 kitten among 518 lynx trapped during a 3-year period of hare scarcity in Alberta. During the first year of decline in hare numbers, yearling and 2-year-old lynx comprised 85% of the harvest; during the second year, 2- and 3-year-olds made up 78% of the harvest; and by the third year, the harvest contained 78% 3- and 4-year-olds. As hare numbers declined dramatically from 1971-1976, the mean age of trapped lynx rose from 1.6-3.6 years (Brand and Keith 1979). At southern latitudes, where hare densities are typically low (Dolbeer and Clark 1975), older age individuals ap-

pear to predominate in lynx populations. Britnell et al. (1989, unpubl.) reported an average age of 4.5 years for 14 lynx harvested in Washington from 1976-1981.

Density

In northern regions, where hare populations cycle, lynx populations respond with a 1- to 2-year lag (Breitenmoser et al. 1993; Brand et al. 1976; O'Conner 1986). Increases in prey numbers result in higher densities of lynx from increased reproduction and decreased mortality. Although social intolerance may separate lynx in time and space (Brand et al. 1976), it does not appear to be a major factor limiting their densities (Breitenmoser et al. 1993; Bergerud 1971).

During periods of hare scarcity, lynx congregate around pockets of hare activity, which may result in inflated density estimates for lynx if extrapolated to other habitats (Bergerud 1971; Carbyn and Patriquin 1983; Todd 1985; Ward and Krebs 1985). On the Kenai National Wildlife Refuge, where overall lynx densities were 1/100 km², densities were 2.3/100 km² in an area that burned in 1947 where hare numbers were high (Bailey et al. 1986). Carbyn and Patriquin (1983) reported trappers removing 16 lynx from 3 km² of high-quality habitat during mid-winter. Such focal areas of lynx activity and localized densities may lead to erroneous population estimates when based on trapper interviews or fur harvest returns.

Snow-tracking studies in Alberta showed that lynx densities increased from 2.1-7.5/100 km² as hare numbers increased (Nellis et al. 1972). In the same study area, later workers (Brand and Keith 1979; Brand et al. 1976) observed a 4.3-fold change in lynx densities from 1966-1972, with the highest density of lynx occurring 1 year after the peak in hare numbers. Bergerud (1971) reported a lynx density of 7.7/100 km² on caribou (*Rangifer* spp.) calving grounds during June. In Alaska, Bailey et al. (1986) estimated that lynx trappers removed 10-17/100 km², suggesting that peak densities may have been greater than 20/100 km², a value equivalent to those reported on Cape Breton Island in Nova Scotia (Parker et al. 1983). Using radiotelemetry and snow-tracking to study lynx in Washington, Koehler (1990) estimated lynx densities of 2.3 adults/100 km² and 2.6 adults and kittens/100 km². Radiotelemetry studies also document changing lynx densities in response to changing hare numbers. In the Yukon, Slough and Mowat (1993, unpubl.) found that densities increased from 2.8/100 km² in 1987 to 37.2/100 km² in 1991 as hare

numbers increased, and then decreased to $< 5/100 \text{ km}^2$ as hare numbers declined. Poole (1993, unpubl.) observed decreases in lynx densities from 35-2/100 km^2 in the Northwest Territories during the same period.

Changes in lynx densities may also be a function of intensity of exploitation. Densities were only 1/100 km^2 on the Kenai National Wildlife Refuge where populations were depleted from heavy trapping pressure (Bailey et al. 1986). After trapping was closed on the refuge, lynx densities increased 4-fold (1.6-6.8/100 km^2) during a period when hare densities were relatively stable (Kesterson 1988). During hare population declines, lynx become increasingly vulnerable to trappers as they expand their movements in search of alternate sources of prey (Brand and Keith 1979).

Management Considerations

1. The lack of dramatic fluctuations in lynx and snowshoe hare populations at southern latitudes will require management approaches that are different from those applied in northern boreal forests where populations are cyclic.

2. In the western mountains, the management of habitat for snowshoe hares is likely to be an important component of lynx conservation efforts due to the relatively low hare densities typical of boreal habitats in the western mountains, and because of the importance of hare availability for successful reproduction.

3. Due to its additive nature, trapping mortality can have significant short-term effects on lynx populations in the western mountains.

Research Needs

1. Implement monitoring and intensive research on lynx and snowshoe hare populations in the western mountains to determine the nature of their population dynamics and to understand why they do not exhibit dramatic fluctuations in numbers over time.

2. Where lynx are harvested in the western mountains, carcasses should be collected and age, sex, and reproductive data gathered.

FOOD HABITS AND PREDATOR-PREY RELATIONSHIPS

Foraging Ecology

Lynx occur in habitats where snowshoe hares are most abundant (Bailey et al. 1986; Bergerud 1971; Koehler 1990; Koehler et al. 1979; Parker et al. 1983;

Ward and Krebs 1985). During periods of hare scarcity, lynx concentrate their activities in pockets of hare abundance (Bergerud 1971; Todd 1985; Ward and Krebs 1985), which are typically dense, brushy sites where hares seek refuge (Wolff 1980). Carbyn and Patriquin (1983) reported 16 lynx being trapped in an area 3 km^2 in extent.

Lynx apparently invest a great deal in learning to hunt, since kittens typically remain with their mother until they are 9-10 months of age (Bailey et al. 1986; Brand et al. 1976; Carbyn and Patriquin 1983; Koehler 1990; Koehler et al. 1979; Parker et al. 1983; Saunders 1963b). Their proficiency at hunting during their first 2 years is critical. When female lynx with kittens are trapped, the kittens are particularly vulnerable to starvation (Carbyn and Patriquin 1983).

When lynx are traveling, most of the time they are searching for food (Brand et al. 1976). Saunders (1963b) reported lynx to be most active from evening until early morning, although Parker et al. (1983) found that radio-collared lynx traveled during both day and night. The distance traveled during hunts, as determined by distances traveled between day-time beds, can vary from 8.8 km when hares are scarce to 4.7 km when hares are plentiful (Brand et al. 1976; Nellis and Keith 1968). Ward and Krebs (1985), however, found no significant difference in distances traveled per day until hare densities dropped below 1.0/ha. Parker et al. (1983) calculated daily cruising distances of 6.5-8.8 km in winter and 7.3-10.1 km during summer in Nova Scotia. In north-central Washington, females foraged up to 6-7 km from their den sites (Koehler 1990).

Cover is important for lynx to stalk prey. From snow-tracking, Brand et al. (1976) determined that lynx encountered and captured hares by following well-used hare runways, concentrating their movements in small areas of hare activity, or using short term "waiting-beds" (typically depressions in the snow) that were usually located near areas of hare activity. When numbers were declining, Brand et al. (1976) found lynx using waiting beds as a hunting strategy more frequently, and Saunders (1963b) reported that this strategy accounted for 61% of hares killed by lynx.

Prey Requirements and Hunting Success

Lynx are specialized predators of snowshoe hares, but they also forage opportunistically, preying on a variety of species as availability of resources change.

Most snow-tracking studies show the importance of hares to the lynx diet, even when hares are scarce and capture rates decrease (table 1). In Nova Scotia, Parker et al. (1983) found that 198 of 200 chases and 34 of 36 kills were of snowshoe hares, whereas in the Yukon, lynx were successful at capturing hares on 32 of 52 occasions (Murray and Boutin 1991). Among 361 attempts to kill prey in central Alberta, 73% were hares and 15% were ruffed grouse (*Bonasa umbellus*) (Brand et al. 1976). Hunting success did not differ among years as hare densities varied, averaging 24% during winters when hares were abundant, and 24-36% when hare numbers were low; capture rates for tree squirrels, however, varied from 0-67% (Brand et al. 1976; Nellis and Keith 1968). Snow-tracking lynx for 20.5 km in north-central Washington, Koehler (1990) detected 2 captures of hares in 6 attempts, and 2 unsuccessful attempts to capture red squirrels. Nellis and Keith (1968) believed that success in capturing hares was a function of snow conditions, experience, and familiarity with the area. Hunting success has also been shown to increase from 14-55% as the size of groups (usually a female and her kittens) increases from 1 to 4 (Parker et al. 1983).

Snow-tracking lynx in Alberta for 416 km, Nellis and Keith (1968) found lynx made 0.42 kills per day, less than half that reported by Parker et al. (1983) for lynx in Nova Scotia. Nellis et al. (1972) calculated a consumption rate of 593 g/day, which is similar to the 600 g/day calculated by Saunders (1963a). During a decline in hare numbers, the mean daily consumption rate of individual lynx may decrease by 37% (Brand et al. 1976). Nellis et al. (1972) found that a captive juvenile required about 370 gm/day of hares, tree squirrels, and birds to increase its body weight from 4.9 to 5.6 kg. This captive juvenile was smaller than recaptured wild littermates, suggesting that wild juveniles may require at least 400 g/day to meet requirements for growth. Because the biomass of a grouse is equal to 0.5 hares and that of a tree squirrel to 0.2 hares (Nellis and Keith 1968), a shift to alternate food sources as hare populations decline may not compensate for the decrease in biomass of hares killed.

Lynx will occasionally prey on ungulates (Bergerud 1971; Koehler 1990; Stephenson et al. 1991), but the importance of ungulates in the diet appears to be insignificant. Bergerud (1971) found caribou calves to be more vulnerable to lynx predation during July and August when newborn calves are led by cows from open habitats to forested sites. Of 33 lynx scats collected on calving grounds, 13 contained

caribou hair (Bergerud 1971). Saunders (1963a) and Bailey (pers. comm.) observed lynx scavenging moose (*Alces alces*) carcasses, and remains of deer (*Odocoileus* spp.) were infrequently found in lynx scats in Washington (Koehler 1990) and Nova Scotia (Parker et al. 1983). Whether the presence of deer hair in scats was from predation or scavenging is unknown.

Temporal and Spatial Variations in Diet

Studies in Alberta (Brand et al. 1976; Brand and Keith 1979; Nellis and Keith 1968, Nellis et al. 1972) have shown that although snowshoe hares make up the greatest biomass of prey consumed throughout the year, lynx use alternate prey during periods of hare scarcity and during the summer and fall seasons. Staples and Bailey (1993, unpubl.) and Saunders (1963a) also found a greater incidence of voles in lynx diets during summer (15-30%) than in winter (5-9%). Brand et al. (1976) reported that snowshoe hares represented only 27 of 71 food items during the summer, compared to 112 of 140 items in winter. In contrast, mice and voles represented 33 of 71 food items during summer, but only 22 of 140 during winter. Despite increased consumption of mice and voles during summer and fall, however, hares still comprised 91% of biomass consumed.

Brand and Keith (1979) observed a decline from 90 to 35% in the frequency of occurrence of hare remains in the diet as hares became scarce. However, the percent biomass of hares remained high, comprising 97% of the total biomass consumed when hares were abundant, and 65% when hares were scarce. During a decline in hare numbers, the frequency of voles and mice shifted from 4 to 28% of the diet and occurrence of tree squirrels increased from 9 to 12%. However, the percent biomass consumed of these species did not change much during the hare decline, remaining 3% for squirrels and 1% for mice and voles. In the only food habits study of lynx conducted in the western mountains, Koehler (1990) found that tree squirrels represented 24% of the food items found in 29 scats in his study area in north-central Washington; remains of tree squirrels were also found at den sites. Staples and Bailey (1993, unpubl.) found a similarly high percentage of squirrels in the diet of lynx in Alaska (28%) during a hare population low (table 1), providing additional evidence that lynx ecology in the western mountains is similar to that occurring in northern latitudes during lows in the snowshoe hare cycle.

Management Considerations

1. In the western mountains, prey species other than snowshoe hares, including tree squirrels, voles, and mice, appear to provide important alternate food sources for lynx.

Research Needs

1. Intensive studies of the food habits of lynx during all seasons of the year in the western mountains are urgently needed.

2. Determine the composition and structure of habitats in the western mountains that provide both sufficient food and cover for hares and adequate stalking cover for lynx.

HABITAT RELATIONSHIPS

Components of Lynx Habitat

From the coast of western Alaska to the eastern islands of Canada and the mountains of the western United States, the distribution of lynx is tied to boreal forests. Lynx occupy habitats at 122 m elevation dominated with white (*Picea glauca*) and black spruce (*P. mariana*), paper birch (*Betula papyrifera*), willow (*Salix* spp.), and quaking aspen (*Populus tremuloides*) on the Kenai Peninsula of Alaska (Bailey et al. 1986); white spruce-dominated forests in southwestern Yukon (Ward and Krebs 1985); aspen, poplar (*P. balsami fera*), and spruce stands in central Alberta (Brand et al. 1976); aspen forests in Manitoba (Carbyn and Patriquin 1983); balsam fir (*A. balsamea*), white spruce, black spruce, and paper birch forests to 390 m elevation on Cape Breton Island, Nova Scotia (Parker et al. 1983); jack pine (*Pinus banksiana*), balsam fir, black spruce, aspen, and paper birch forests in northern Minnesota (Mech 1980); Engelmann spruce (*P. engelmannii*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*P. contorta*), and aspen forests above 1,463 m in north-central Washington (Koehler 1990); and similar forest communities in western Montana (Koehler et al. 1979). They occur in the Rocky Mountains above 1,900 m elevation in Wyoming and above 2,400 m in Colorado and Utah (Koehler and Brittell 1990).

In these habitats, lynx typically occur where low topographic relief creates continuous forest communities of varying stand ages. These features are most prevalent at northern latitudes but they also appear

to be important components of lynx habitat in the mountains of the western United States. In both areas, such conditions are important for maintaining hare populations needed to support stable lynx populations. Habitat continuity, or the degree of habitat fragmentation, may also influence lynx population dynamics. Vast expanses of successional forests at northern latitudes support periodic population booms and crashes in numbers of hares. At southern latitudes, however, habitats are more fragmented and discontinuous resulting in lower, but more stable, hare populations (Chitty 1950; Dolbeer and Clark 1975; Koehler 1990; Sievert and Keith 1985; Windberg and Keith 1978; Wolfe et al. 1982; Wolff 1980).

Lynx habitat in the western mountains consists primarily of two structurally different forest types occurring at opposite ends of the stand age gradient. Lynx require early successional forests that contain high numbers of prey (especially snowshoe hares) for foraging and late-successional forests that contain cover for kittens (especially deadfalls) and for denning (Brittell et al. 1989, unpubl.; Koehler and Brittell 1990). Intermediate successional stages may serve as travel cover for lynx but function primarily to provide connectivity within a forest landscape. Although such habitats are not required by lynx, they "fill in the gaps" between foraging and denning habitat within a landscape mosaic of forest successional stages.

Foraging Habitat

Stand Age

Early successional forests where snowshoe hares are plentiful are the habitats that lynx favor for hunting. Such forests may result from fires (Bailey et al. 1986; Fox 1978; Keith and Surrendi 1971; Koehler 1990, 1991), timber harvesting (Conroy et al. 1979; Koehler 1990, 1991; Litvaitis et al. 1985; Monthey 1986; Parker et al. 1983; Wolfe et al. 1982), or windthrow and disease (Koehler and Brittell 1990).

Based on hare pellet counts in Washington, Koehler (1990) found that hares were more abundant in younger-aged stands of lodgepole pine than in any other forest type. Hares were 4-5 times more abundant in 20-year-old lodgepole pine stands than in 43- and 80-year-old stands, and 9 times more abundant than in stands >100 years old. In Newfoundland, hares began to use cutover areas when stands reached 10 years of age, but frequency of use peaked when the stands were 22 years old (Dodds 1960). In Nova

Scotia, Parker et al. (1983) estimated hare densities at 10/ha in mid-successional habitats (16-30 years old), compared to 5.8/ha in mature conifer habitats. In Maine, hare activity was greater in 12- to 15-year-old clearcuts than in younger stages (Monthey 1986). On the Kenai National Wildlife Refuge in Alaska, hares used areas burned in 1947 more intensively than alder-dominated stands, an area burned in 1969, or mature forests, presumably because the latter habitats lacked adequate food and cover (Bailey et al. 1986).

Stand structure appears to strongly influence recolonization by hares. One year after a wildfire in Alberta, where prefire cover density was 86%, hares recolonized an intensively burned site after seedling and shrub cover approached 61% (Keith and Surrendi 1971). In this study, aspen and balsam poplar recovered quickly by sprouting. This contrasts to findings in Maine where clearcut areas initially experienced a decline in hares, and it wasn't until 6-7 years after spruce and fir became reestablished that hares recolonized the area, peaking in numbers 20-25 years later (Litvaitis et al. 1985). Litvaitis et al. (1985) found that clearcutting improved habitat quality for hares in mature forest stands where understory stem density was low.

The capacity of burned areas to support high densities of hares, and therefore lynx, undoubtedly declines over time (Fox 1978). Because succession progresses slowly at northern latitudes, older-aged (~40 years old) stands there may provide optimal conditions for hares, whereas at southern latitudes, younger-aged stands (15-30 years old) appear to provide the best habitat for hares.

Tree Species Composition

Conifer stands provide greater concealment from predators, lighter snowpacks, and warmer temperatures during winter than hardwood stands (Fuller and Heisey 1986). In Minnesota, hares used habitats with a conifer overstory and a low-growing understory, a pattern that was particularly evident during periods of hare scarcity (Fuller and Heisey 1986). Conifer cover proved to be an important habitat component for hares during a decline in Nova Scotia as well (Parker et al. 1983). In Alaska, thickets that served as refugia during periods of hare scarcity were dominated by black spruce, whereas burned areas dominated by herbaceous woody plants were occupied only during periods of hare abundance (Wolff 1980). In Maine, Monthey (1986) observed hares selecting conifer stands and Litvaitis et al. (1985) found

that individual conifer stems provided about 3 times more cover than leafless hardwood stems. They also documented a strong positive correlation between the number of hares live-captured in the spring and the density of conifer stems; there was no statistical correlation with the density of hardwoods or with total stem density. Wolfe et al. (1982) concluded that dense stands of aspen in the Rocky Mountains represented marginal habitat for hares because such stands do not provide adequate cover. These studies strongly indicate that conifer cover is critical for hares during the winter.

Litvaitis et al. (1985), however, found that in coastal locations in Maine, hares preferred low-density hardwood stands where lateral foliage density was greater than in conifer stands, and that hares avoided mixed stands with an open understory. In the mountainous inland region of the state, however, hares preferred conifer stands with higher stem densities than those found in hardwood stands.

Even at southern latitudes, where hare population cycles may not occur, conifer cover is an important habitat component (Dolbeer and Clark 1975; Koehler 1990; Pietz and Tester 1983). In Colorado and Utah, dense stands of subalpine fir and Engelmann spruce and Douglas-fir were used most frequently by hares (Dolbeer and Clark 1975; Wolfe et al. 1982); in Montana, dense stands of Douglas-fir were selected (Adams 1959); and in Washington, dense stands of lodgepole pine were used most often (Koehler 1990, 1991), indicating that stem density is more important to hares than species of conifer.

Stem Density

In Washington, Koehler (1990) found a significant correlation between hare densities and stands with tree and shrub stems that were less than 2.5 cm in diameter at breast height (DBH); intensively used 20-year-old stands had 15,840 stems/ha (1.6 stems/m²). In Alaska, Wolff (1980) found that hares preferred stands with tree and shrub densities of 22,027 stems/ha, and in Nova Scotia, hares frequented stands with stem densities of 9,000 conifers/ha (0.9/m²) and 7,000 hardwoods/ha (0.7/m²) (Parker et al. 1983). In Maine, hares preferred stands dominated with stems > 0.5 m tall and ≤ 7.5 cm DBH at densities > 16,000 stems/ha (1.6/m²), with an understory visual obstruction > 60% (Litvaitis et al. 1985). Monthey (1986) also found hares to be common in densely stocked stands (stems < 8.9 cm DBH and > 0.6 m tall with 6,000-31,667 stems/ha [0.6-3.2 stems/m²]) in Maine. In Utah, hares

seldom used stands with understories having < 40% visual obstruction during winter (Wolfe et al. 1982).

Stem Height

Because snow depths typically exceed 1 m in boreal forests, the height of stems is also an important component of winter habitat. In Minnesota, Pietz and Tester (1983) found a positive correlation between the percentage of shrub cover > 1 m tall and numbers of winter hare pellets. In Nova Scotia, habitats with stem heights between 2-3 m were important for hares, whereas mature forests with stem heights of 6-8 m and browse height < 1.0 m provided inadequate winter habitat (Parker et al. 1983). In the Rocky Mountains, where snow depths may exceed 1.5 m, Dolbeer and Clark (1975) found that sparsely stocked stands provided little food or cover, and Wolfe et al. (1982) reported that 85% of habitats used by hares had a horizontal cover density of 40% at a height of 1.0-2.5 m above the ground. In central Wisconsin, however, where snow depths may be less, Sievert and Keith (1985) concluded that stands with a dense cover of stems < 1.5-m tall provided good habitat for hares.

During snow-free periods, thermal cover is not a critical factor and alternate sources of food are available. During these times, hares will occupy habitats that are more open and where hardwoods and herbaceous vegetation are more prevalent (Dodds 1960; Litvaitis et al. 1985; Parker et al. 1983; Wolfe et al. 1982). During snow-free months, Parker et al. (1983) and Adams (1959) reported that hares avoided very dense stands where shade created by a dense canopy reduces the growth of herbaceous understory vegetation.

Denning Habitat

For denning, females select dense, mature forest habitats that contain large woody debris, such as fallen trees or upturned stumps, to provide security and thermal cover for kittens (Berrie 1973; Koehler 1990; Koehler and Brittell 1990; Kesterton 1988; Murie 1963). In north-central Washington, lynx denned in stands \geq 200 years old with Engelmann spruce-subalpine fir-lodgepole pine overstories having N-NE aspects; these sites also had a high density (> 1/m) of downed trees supported 0.3-1.2 m above the ground, which provided both vertical and horizontal structural diversity (Brittell et al. 1989, unpubl.; Koehler 1990). Other important features of denning sites are minimal human disturbance, proximity to foraging habitat (early successional forests), and

stands that are at least 1 ha in size (Koehler and Brittell 1990). Travel corridors between den sites are important to permit females to move kittens to areas where prey are more abundant or to avoid disturbance (Koehler and Brittell 1990).

In areas where denning habitat is abundant, female lynx often change denning sites during and between seasons (Washington Dept. of Wildlife 1993, unpubl.). Where high-quality denning habitat is scarce, however, lynx may re-use the same denning site (pers. Comms. By Brittell and Slough cited in Washington Dept. of Wildlife 1993, unpubl.). The availability of alternate den sites may be an important determinant of habitat quality. In low-quality habitat, the inability of females to move kittens to alternate dens when danger threatens may increase mortality rates for kittens. According to Brittell et al. (1989, unpubl.), den sites consisting of mature forest habitat are also important for lynx as refugia from inclement winter weather or drought.

Travel Cover

Like most wild felids, lynx require cover for security and for stalking prey; they avoid large, open areas. Although lynx will cross openings \leq 100 m in width, they do not hunt in these areas (Koehler 1990; Koehler and Brittell 1990). Travel cover allows for movement of lynx within their home ranges and provides access to denning sites and foraging habitats (Brittell et al. 1989, unpubl.). In general, suitable travel cover consists of coniferous or deciduous vegetation > 2 m in height with a closed canopy that is adjacent to foraging habitats (Brittell et al. 1989, unpubl.). Lynx are known to move long distances but open areas, whether human-made or natural, will discourage use by lynx and disrupt their movements. Thus, maintaining travel corridors between populations may be important to ensure the long-term viability of peripheral or isolated populations in the western mountains (Koehler 1990; Koehler and Brittell 1990).

Roads constructed for forest management, mining, or recreational purposes may increase the vulnerability of lynx to hunters and trappers (Bailey et al. 1986; Todd 1985) and increase opportunities for accidental road deaths (Brocke et al. 1992). During winter and summer, lynx frequently travel along roadways with < 15 m right-of-ways, where adequate cover is present on both sides of the road (Koehler and Brittell 1990). Although forbs, grasses, and shrubs that grow along edges of roads can benefit hares and attract

lynx, increased access and use of roadways by people may pose a threat to lynx populations, particularly during times of high pelt prices and low recruitment (Bailey et al. 1986).

Although sparsely stocked stands are poor habitat for hares, they may benefit lynx by serving as dispersal sinks in which juvenile hares are more vulnerable to predation (Dolbeer and Clark 1975; Sievert and Keith 1985; Windberg and Keith 1978). For these reasons, an interspersed of dense stands that provide refugia for hares, and sparsely stocked stands where hares are more vulnerable, may be more beneficial to lynx than a continuous distribution of optimal hare habitat.

Because plant succession progresses more rapidly at southern latitudes, small-scale disturbances at frequent intervals may be necessary to provide for a temporal continuum of stand ages. Fires, epidemics of forest disease, and logging may have negative short-term effects by eliminating cover for snowshoe hares and lynx, but will have long-term benefits as succession progresses, cover is restored, and snowshoe hares become abundant (Koehler and Brittell 1990; Parker et al. 1983).

Management Considerations

1. High-quality lynx habitat in the western mountains consists of a mosaic of early successional habitats with high hare densities, and late-successional stands with downed woody debris for thermal and security cover and for denning.

2. Clearcuts >100 m wide may create barriers to lynx movements.

3. Hares may not begin to recolonize Clearcuts until 6-7 years after cutting, thus it may take 20-25 years at southern latitudes for snowshoe hare densities to reach highest levels.

4. Thinning stands early to maximize tree-growth potential can be compatible with snowshoe hare and lynx habitat needs provided that stands are thinned before snowshoe hares recolonize the area. Otherwise, thinning may be most effective when stands are older than 30-40 years and are used little by hares. Both early and late thinning strategies may be required when integrating timber management objectives with lynx habitat needs.

5. Small-sized parcels (1-2 ha) of late-successional forest appear to be adequate for den sites, but these parcels must be connected by corridors of cover to permit females to move kittens to alternate den sites providing suitable access to prey.

6. Approximating the natural disturbance frequency and spatial patterns present on the landscape is expected to provide the best habitat for lynx. Frequent, small-scale disturbances is expected to provide the best lynx habitat at southern latitudes.

7. Although disease and insect attacks may increase fuel loads and the risk of large, high-intensity fires, they also provide dead and downed trees used for denning cover. Thus, the role that disease and insects play in the dynamics of forests being manipulated must be carefully considered when managing stands for timber and lynx.

8. Road management is an important component of lynx habitat management. Although construction and maintenance of roads both destroys and creates habitat for prey, lynx use roads for hunting and travel which may make them more vulnerable to human-caused mortality.

Research Needs

1. Studies of lynx distribution and habitat use in the western mountains are urgently needed. Gathering this information will require winter surveying of remote areas in winter where lynx are believed to occur and evaluating patterns of occurrence with geographic information systems (GIS). GIS can then be used to inventory available habitats on a regional scale. Once this is achieved, more intensive field investigations of habitat use, spatial patterns, and reproductive ecology using radiotelemetry will be appropriate.

2. Forest management activities, timber harvesting, and prescribed and wild fires can be either detrimental or beneficial to lynx, depending upon their scale and dispersion on the landscape. Although guidelines exist, it will require some experimentation to determine prescriptions that provide an optimal range and pattern of habitat patchiness to benefit both hares and lynx. Such experimentation will require long-term research and monitoring of both lynx and snowshoe hare populations.

HOME RANGE AND MOVEMENTS

Home Range

Lynx partition resources both spatially and temporally, but determining the social and spatial organization of solitary felids is difficult. Most studies do not encompass a long enough time period nor do they include an adequate sample of individuals. These

limitations result from the difficulties involved in (1) capturing and marking individuals occupying adjacent home ranges, and (2) obtaining representative samples of sex and age classes. However, certain patterns can be detected from the studies that have been conducted. Although lynx are considered to be solitary, they frequently travel in groups, such as females with kittens, two adult females with their litters, or females traveling with males during the breeding season (Carbyn and Patriquin 1983; Parker et al. 1983; Saunders 1963b).

Snow-tracking and radiotelemetry studies have been used to delineate spatial requirements of lynx and to assess spatial partitioning between and within sexes. Nellis et al. (1972) identified areas used by lynx as activity centers that were separated in time and space. Radiotracking studies by Parker et al. (1983) support the concept of lynx using activity centers during winter. They documented both males and females concentrating 75% of their activity in core areas, which ranged from 35-63% of winter home ranges. Although in Alaska, Kesterson (1988) found that lynx in Alaska occupied intrasexually exclusive areas, spatial overlap among individuals is common (Bergerud 1971; Brand and Keith 1979; Koehler 1990; Saunders 1963b; Ward and Krebs 1985), and it is generally believed that lynx occupy home range areas rather than exclusive territories.

Factors that influence the size and shape of home ranges are not fully understood, but it is generally believed to be related to the availability of prey and the density of lynx. Other factors that may contribute to the size and configuration of home range areas include geographic and physiographic features. Saunders (1963b) found that home range boundaries coincided with habitat features, and Koehler (unpubl. data) observed home range areas in a mountainous region of Washington to correspond to drainage patterns, with home range boundaries generally occurring along ridges and major streams. Therefore, physiographic features and variation in the distribution of habitats may partially account for differences in home range sizes between geographic areas.

Ward and Krebs (1985) demonstrated a correlation between prey density and lynx home range sizes in the Yukon by using radiotelemetry. As numbers of hares decreased from 14.7 to < 1 /ha, the mean home range size for lynx increased from 13.2 to 39.2 km², a 3-fold increase in home range size in response to a 14-fold decrease in hare abundance. Similarly, Poole (1993, unpubl.) found lynx home ranges increased

from 17 km² to 25-84 km² as hare numbers dropped, with the majority of lynx becoming nomadic or emigrating at that time. Such observations of lynx changing their use of space in response to declining numbers of hares is in contrast to findings by Breitenmoser et al. (1993), however, which showed no change in the size of home ranges between periods of high and low hare numbers. In addition, snow-tracking studies by Brand et al. (1976) indicated that lynx did not modify their home range sizes in response to changing numbers of hares. However, during a period of low hare densities in interior Alaska, Perham et al. (1993, unpubl.) observed some lynx hunting in isolated pockets of hare activity and occupying small home ranges, whereas others became nomadic or emigrated. Slough and Mowat (1993, unpubl.) found that mean annual home range sizes varied from 8.3 to 18.2 km² for females and from 17.3 to 51.0 km² for males as hare numbers increased from 1982 to 1992. They hypothesized that lynx maintained intrasexual territories during hare lows, but that this intolerance broke down as hare numbers increased.

A variety of techniques has been used to calculate the size of home range areas, and each technique can result in different estimates. For example, snow-tracking generally results in smaller home ranges from those calculated from radiotelemetry studies. Furthermore, the number of locations used generally differs between studies and can affect area determination (Mech 1980; White and Garrott 1990). For these reasons, caution must be applied when comparing home range sizes between different studies.

Studies using radiotelemetry have estimated home ranges for lynx varying in size from 8 to 783 km² (Berrie 1973; Bailey et al. 1986; Brainerd 1985; Brittell et al. 1989, unpubl.; Carbyn and Patriquin 1983; Kesterson 1988; Koehler 1990; Koehler et al. 1979; Parker et al. 1983; Perham et al. 1993, unpubl.; Poole 1993, unpubl.; Slough and Mowat 1993, unpubl.; Smith 1984; Ward and Krebs 1985). Based on snow-tracking, lynx occupy areas from 15.4 to 20.5 km² in Newfoundland (Saunders 1963b), and 18 to 49 (average 38.4) km² in Alberta (Nellis et al. 1972). On the same study area in Alberta, Brand et al. (1976) estimated that home range size varied from 11.1 to 49.5 km² (average 28.0 km²).

Although large home ranges are generally associated with low numbers of prey, they may also occur in areas into which lynx have recently immigrated (Mech 1980) or that are heavily trapped (Bailey et al. 1986; Carbyn and Patriquin 1983). In Manitoba, home

ranges used by two females during winter averaged 156 km² while that for a male was 221 km² in an area that was intensively trapped (Carbyn and Patriquin 1983). Their study area of 2,144 km² was an isolated refuge surrounded by agricultural land that was only occasionally colonized by immigrating lynx. On the Kenai Peninsula in Alaska, where lynx were heavily exploited, Bailey et al. (1986) found home ranges for two females to be 51 and 89 km² and that for one male to be 783 km². As lynx densities increased after the trapping season was closed, sizes of lynx seasonal home ranges decreased 54.7% for resident males and 36.9% for nondenning, resident females (Kesterson 1988). During a period of increasing hare numbers in Nova Scotia, an adult female used an area of 32.3 km² and an adult male, 25.6 km² (Parker et al. (1983).

Lynx that had immigrated into Minnesota where hares were scarce occupied areas of 51-122 km² for females and 145-243 km² for males (Mech 1980). Lynx translocated to an area of low hare density (mean of 0.5 hares/ha) in New York also had large home ranges, with harmonic mean estimates of 1,760 km² for 21 males and 421 km² for 29 females (Brocke et al. 1992). In this area, 73% of known mortalities were human-caused. This high level of mortality was believed to have resulted from fragmented property ownership and many access roads. In Washington, where hares were relatively scarce and suitable habitats scattered, home range sizes averaged 39 km² for 2 females and 69 km² for 5 males (Koehler 1990). In western Montana, the mean home range size for 4 lynx (2 males and 2 females) was 133 km² (Smith 1984). In a subsequent study in the same area, Brainerd (1985) radio-collared 7 lynx and measured mean annual home ranges of 122 km² for males and 43.1 km² for females.

Lynx will maintain home ranges for several years. In Washington, site fidelity was observed for more than 2 years (Koehler 1990) and in the Yukon, a male was observed using the same area for at least 10 years (Breitenmoser et al. 1993). Radiotelemetry studies show that home range sizes vary by season. In Alaska, females occupied smaller areas in summer (25 km²) than in winter (49 km²) (Bailey et al. 1986). The opposite relationship was documented in Nova Scotia, however, where an adult female expanded her home range from 18.6 km² in winter to 32.3 km² in summer, and an adult male from 12.3 km² in winter to 25.6 km² in summer; there was little seasonal change for a juvenile (10.1 km² in winter and 7.9 km² in summer) (Parker et al. 1983). Prior to dispersing,

a juvenile male occupied a home range in Alaska of 8.3 km² in an area providing high-quality hare habitat (Bailey et al. 1986). In one of the few studies conducted in mountainous terrain, Koehler (1990) found that lynx in north-central Washington used significantly higher elevations during summer (range 1,463-2,133 m) than in winter (range 1,556-2,024 m). The extent of home range overlap for lynx is variable. Ward and Krebs (1985) found male home ranges to overlap those of other males by 10.5%, among females by 24.5%, and between males and females by 22.0%. However, in Washington, Koehler (1990) found home ranges of males and females to overlap completely, particularly during March and April when breeding occurred (Koehler, unpubl. data). Parker et al. (1983) also documented complete overlap in home ranges of radio-collared males and females, and Mech (1980) found complete overlap among radio-collared females but not among males, although there may have been overlap with uncollared males. Kesterson (1988), however, observed little overlap in home range use among females (mean overlap, 5.0%) or among males (3.8%); however, male ranges overlapped those of 1-3 females.

Movements and Dispersal

When hares are scarce, several lynx may congregate around pockets of dense vegetation or on caribou calving grounds where prey resources are more plentiful (Bergerud 1971; Ward and Krebs 1985). During such times, the spatial and temporal segregation of lynx may cease to exist, and some lynx may abandon their home range areas and become nomadic or emigrate in search of prey (Poole 1993, unpubl.; Ward and Krebs 1985). Records indicate long-distance movements by lynx of 1,100 km (Slough and Mowat 1993, unpubl.) and 700 km (Ward and Krebs 1985) in the Yukon, 930 km in the Northwest Territories (Poole 1993, unpubl.), 616 km in Washington (Brittall et al. 1989, unpubl.), 325 km in western Montana (Brainerd 1985), 483 km in Minnesota (Mech 1977), 164 km in Alberta (Nellis et al. 1972), and 103 km in Newfoundland (Saunders 1963b). Translocated lynx in New York used areas exceeding 1,000 km² (Brocke et al. 1992).

Ward and Krebs (1985) considered the abandonment of home range areas and nomadic behavior to be related to decreased hare densities, especially when hare densities dropped below 0.5/ha. In the Yukon, Slough and Mowat (1993, unpubl.) found

annual immigration and emigration rates to be relatively constant at 10-15%, with most juvenile males dispersing and juvenile females tending to remain on their natal ranges, although emigration increased to 65% with no apparent immigration as hare numbers crashed. In the Northwest Territories, kittens and yearlings began dispersing during the peak in hare numbers, while emigration of adults didn't occur until after the crash in hare numbers (Poole 1993, unpubl.).

These long-range movements may serve to repopulate vacated areas or to augment depauperate populations along the southern edge of the lynx's range. After a long period of heavy trapping pressure, lynx populations increased during the 1960's in Alberta (Todd 1985) and in eastern Montana (Hoffmann et al. 1969). As is indicated by the failure of lynx to establish themselves in Minnesota after immigrating- there in large numbers in the early 1970's (Mech 1980), however, such movements are unlikely to result in stable lynx populations unless available habitats are capable of supporting both snowshoe hares and lynx in sufficient numbers for population persistence.

During the 1970's, heavy trapping pressure probably resulted in overexploitation of lynx populations in Ferry County, Washington, yet only recently does it appear that lynx have recolonized that area (Washington Dept. of Wildlife 1993, unpubl.; Koehler, pers. obs.). Lynx habitat in Ferry County is separated from suitable habitat in British Columbia by the Kettle River drainage and xeric non-lynx habitats that may act as barriers to lynx dispersal and recolonization. Extensive fires, logged areas, and forest disease control programs may also act to inhibit immigration of lynx into suitable habitat (Koehler 1990; Koehler and Britnell 1990).

Translocation may be a viable alternative for reestablishing lynx populations into areas where they occurred historically, but reintroductions are problematic. Of 50 lynx translocated from Yukon Territory to the Adirondack Mountains of New York, 6 animals were killed on roads, 2 were shot, and 3 young lynx died from natural causes (Brocke et al. 1992). The home range sizes of translocated animals were very large, averaging 1,760 km² for males and 421 km² for females, suggesting that they exhibited the unsettled behavior of recently translocated animals, which may make them more vulnerable to both human-related and natural mortality (Brocke et al. 1992). The authors suggest that large, continuous

blocks of public land, with minimal development or roads providing vehicular access, will be critical for the survival of reintroduced lynx.

Management Considerations

1. Differences in the home range requirements and social organization of lynx in different areas indicate that management is best considered at regional levels, rather than provincial or state levels. Considering the role that emigration may play in population dynamics at a regional scale, it is also important to recognize that management activities in one area may affect populations in neighboring and outlying regions.

2. Habitat management for lynx would benefit from a consideration of local home range sizes and distributions, and vegetative and physiographic features which may serve as home range boundaries.

Research Needs

1. Many authors have suggested that periodic interruptions of lynx in Canada, resulting in the emigration of lynx to peripheral areas outside of their core range, are an essential factor in the maintenance of marginal populations. Although they will be extremely difficult to conduct, studies are needed to assess the importance of immigration on the demographics and persistence of peripheral populations.

COMMUNITY INTERACTIONS

The lynx is a specialized predator of snowshoe hares; its geographic distribution, the habitats it selects, its foraging behavior, reproductive capacity, and population density are all affected by the distribution and abundance of the snowshoe hare. The snowshoe hare is also an important part of the diet of several other predators in boreal forests of North America. In central Canada, hares may comprise 20.4-51.8% of the winter diet of marten (*Martes americana*) (Bateman 1986; Thompson and Colgan 1987) and hares are also potentially important in the diets of fishers (*Martes pennanti*) and, to a lesser extent, wolverines (*Gulo gulo*). Their different foraging strategies and use of habitats, however, may minimize opportunities for competition for prey between these species and lynx (see chapters on marten, fisher, and wolverine). At northern latitudes, coyotes, red foxes, and several species of raptors also prey on

hares, and at southern latitudes, bobcats may also be significant competitors.

Other mammalian predators and raptors that prey on hares may contribute to increased mortality and depressed populations of hares, which could affect the availability of prey for lynx (Boutin et al. 1986; Dolbeer and Clark 1975; Keith et al. 1984; Sievert and Keith 1985; Trostel et al. 1987; Wolff 1980). In southwest Yukon, hares comprised 86.2 and 77.0% of coyote and red fox diets, respectively (Theberge and Wedeles 1989). Coyotes also preyed on hares in Alaska during winter, where hares occurred in 16% of coyote scats and 64% of lynx scats examined (Staples and Bailey 1993, unpubl.). Keith et al. (1984) found lynx to kill 0.8 hares/day, coyotes 0.6/day, and great horned owls 0.35/day; half of the mortality of radio-collared hares was attributed to coyote kills. At southern latitudes, Litvaitis and Harrison (1989) found snowshoe hare remains in 64.7-84.0% of bobcat diets and 29.3-66.7% of coyote diets.

Although their diets may overlap, differences in habitat selection may minimize competition for prey resources by lynx and other predators, especially during winter. Measurements show the relative support capacity of lynx paws to be twice that for bobcat paws (Parker et al. 1983) and 4.1-8.8 times that of coyote paws (Murray and Boutin 1991), enabling lynx to exploit high-elevation areas where deep snow would exclude coyotes and bobcats (Brocke et al. 1992; Koehler and Hornocker 1991; Murray and Boutin 1991; Parker et al. 1983). However, opportunities for resource overlap among these species may increase during winter due to increased access to high-elevation habitats via snowmobile trails and roads maintained for winter recreation or forest management activities. Increased competition from other predators may be particularly detrimental to lynx during late winter when hare numbers are lowest and lynx are nutritionally stressed.

Management Considerations

1. Because the ranges of lynx, bobcats, and coyotes overlap in the western mountains, competition for snowshoe hares and other prey species may be of significant management concern.

Research Needs

1. Determine the extent to which lynx compete with other predators for prey, and under what conditions competition may adversely affect lynx populations.

CONSERVATION STATUS IN THE WESTERN MOUNTAINS

Lynx populations in the western mountains of the United States occur at the periphery of the species' range in North America. At high elevations, climatic conditions similar to those occurring at higher latitudes support boreal forests, snowshoe hares, and lynx. Populations in this region, particularly those found in Wyoming, Utah, and Colorado, exist at low densities in fragmented and disjunct distributions. Although habitats at high elevations in the western mountains are sufficient to support this boreal community, ecological conditions there vary in significant ways from those in boreal regions of Canada and Alaska. Because of the fragmented nature of habitat and the presence of facultative predators and potential competitors in the western mountains, snowshoe hare populations and, consequently, lynx populations do not exhibit dramatic population cycles (Koehler 1990). In the western mountains, populations of both species occur at densities comparable to those found during hare population lows in Canada and Alaska. Additionally, available evidence indicates that lynx food habits, natality and mortality rates, habitat use, and spatial patterns in the western mountains are comparable to those occurring in the north when hare populations are at low densities.

Lynx are vulnerable to trapping, and the effect of trapping mortality on population numbers appears to be largely additive, not compensatory. Brand and Keith (1979) speculated that during hare population lows when recruitment in lynx populations is low, intensive trapping of lynx could result in local extinctions. These authors recommended that trapping of lynx in northern boreal forests should cease during the 3-4 years when hare populations are at their lowest levels. Because hare populations are always at generally low levels in the western mountains, this line of reasoning suggests that complete protection of lynx populations in the western states may be appropriate to ensure their population persistence.

Lynx are protected in Wyoming, Utah, and Colorado, and Washington closed the lynx harvest in 1991 when the north Cascades lynx population was petitioned for federal listing as endangered. The petition was denied (Federal Register 1992, 1993), but Washington State classified the lynx as threatened in October 1993 (Washington Dept. of Wildlife 1993, unpubl.). Lynx are still classified as furbearers in Idaho and Montana, although strict harvest quotas are imposed (table 2).

The range of lynx in the western mountains has diminished over the last century, suggesting that lynx may be negatively impacted by development. Because suitable habitats are more fragmented and restricted in extent in the western mountains, lynx may be less tolerant of human activities there than in Canada and Alaska, where refuge habitats are more prevalent. Thus, providing protected areas within optimal lynx habitat in the western mountains may be important for the persistence of lynx populations. Landscape-level research using radio-telemetry and GIS analyses are needed to study the effects of human activity on lynx populations.

It is of critical importance to the conservation of lynx in the western mountains to evaluate the extent to which these populations are tied to source populations in Canada. Emigrating lynx appear to have very low survival rates. Are southern populations augmented periodically by lynx moving in from the north, or are they simply maintained at low levels by habitat limitations and unaffected by such immigration? Will international cooperation involving lynx population management be required, or should efforts be directed at habitat management at the local or regional level? Answers to these questions will be essential to the design of management strategies for lynx, especially in Washington, Idaho, and Montana.

Only five lynx studies have ever been conducted in the western mountains of the United States, in-

cluding two in Washington and three in Montana (table 3). These studies have been concerned mainly with home range characteristics and habitat use; information on demography, food habits, dispersal, and denning sites is almost totally lacking. Additional research on lynx in the western mountains, especially studies of their foraging ecology, den site characteristics, and habitat relationships at the landscape scale, are urgently needed. The conservation of such a wide-ranging and specialized predator will require a significant commitment of resources to obtain the information needed to maintain viable populations in the western United States.

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Topic, author	Location	Method	Duration	Sample size
Home range and habitat use				
*Brittall et al. 1989, unpubl.	NE Washington	Telemetry (hr) ¹	34 months	15
*Koehler 1990	NE Washington	Telemetry (hr)	25 months	7
*Koehler et al. 1979	NW Montana	Telemetry (hr)	8 months	2
*Smith 1984	W Montana	Telemetry (hr)	23 months	4
*Brainerd 1985	W Montana	Telemetry (hr)	25 months	7
Demography				
Brainerd 1985	W Montana	Carcasses	4 trapping seasons	20
Food habits				
Koehler 1990	NE Washington	Scats	25 months	29
Dispersal				
None				
Natal dens				
Koehler 1990	NE Washington	Telemetry	25 months	4 dens; 2 females

¹ (hr) = home range size reported.

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