# Ecology of Lynx in Northern Canada and Alaska

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**Abstract**—We review the ecology of lynx in the northern part of its range, drawing heavily on the results of recent research from that region. Snowshoe hares form the bulk of prey items in essentially all studies and at all periods in the cycle, but use of alternative prey, often red squirrel, increases as hares become scarce. Caching of freshly killed prey is rare, although carrion is consumed, primarily during periods of food shortage. Habitat use by lynx varies geographically, but tends to track that of snowshoe hares. Lynx prefer older (>20 years old) regenerating forest stands. Mature forest stands are often used but rarely selected. Most lynx dens found to date have been associated with blowdown or deadfall trees in regenerating stands. Lynx maintain mostly exclusive intrasexual territories, based on social intolerance and mutual avoidance. Male home ranges tend to be larger than female ranges. There appears to be no linear relationship between hare abundance and lynx home range size, although lynx do increase their home range size dramatically following the cyclic hare crash. Male and female home ranges generally overlap completely while within-sex overlap is usually modest; related females may

tolerate greater overlap. Lynx numbers fluctuate in synchrony over vast areas and generally lag behind the snowshoe hare cycle by about one year. Peak densities of 30-45 lynx / 100 $km^2$ have been observed in regenerating stands, and 8-20 / 100 $km^2$ in mature forest and more southern ranges. Population densities during the low are <3 lynx / 100 $km^2$. Growth in lynx populations is a result of high fecundity, high kit survival, and low adult mortality. The decline is due to increased dispersal, high natural mortality, and a collapse in recruitment. During hare abundance, adult fecundity is high, litter size averages four to five, and yearling lynx give birth. During the cyclic low, recruitment essentially fails for about two years, and is followed by several years of modest recovery. Although trapping is an important mortality source in many areas, natural causes (primarily starvation and predation) account for most detected mortality during the first two years after the hare decline. Fifteen straight-line dispersal distances of 500-1,100 km have been recorded from recent studies in the two northern territories. Dispersal of adults was highest during and following the decline in hare densities. Trapping can reduce lynx populations and can have the greatest impact during the cyclic low, but the long-term impact of trapping on subsequent cycles is unclear. Despite reduced harvests in all jurisdictions and localized overharvest in some areas, no permanent decrease in range has been detected in contiguous northern populations.

## Introduction

The primary purpose of this chapter is to synthesize relevant information on lynx ecology in northern Canada and Alaska. We have followed the ecoregion domains of Bailey (1998) to divide work covered in this chapter from work conducted in “southern boreal forests” (Chapter 13); here we review research conducted in the polar domain (Bailey 1998). Our intention was to review studies done in a northern boreal environment, as opposed to those done in more southern forests (reviewed by Koehler and Aubry 1994). Much new research on lynx has been conducted over the past decade, most of it from the northern boreal region. This chapter will emphasize these recent studies and will update previous reviews of lynx ecology (e.g., McCord and Cardoza 1982; Tumlison 1987; Quinn and Parker 1987; Hatler 1988, unpublished; Koehler and Aubry 1994). We refer briefly to snowshoe hare ecology primarily as it directly relates to lynx; more comprehensive examinations of the ecology of both northern and southern hare populations are provided in Chapters 6 and 7.

There has been much casual discussion among lynx researchers and managers regarding the similarity of ecological dynamics, processes, and relationships of northern populations of lynx to those residing in montane environments. We make limited comparisons between northern and southern populations here; this will be covered in greater detail in Chapter 13. Here we review lynx behavior in terms of prey selection, foraging patterns, habitat selection, and social organization. We summarize information regarding population dynamics including recruitment, survival, dispersal, and population densities. All topics are presented with respect to the relationship between lynx and snowshoe hare population dynamics. The relationship between lynx and other carnivores of the boreal community are presented elsewhere (Chapter 4).

### Description

The Canada lynx is a medium-sized cat with a flared facial ruff, black ear tufts, large padded feet, and a short, black-tipped tail (Banfield 1974; Quinn and Parker 1987). Lynx show mild sexual dimorphism in size, males (averaging 80-90 cm long and 9-10.5 kg in weight) being 13-25% larger than females (76-84 cm long and 8-9 kg; Quinn and Parker 1987). In the north, lynx are found to the northern limit of trees in Alaska, Yukon, and mainland Northwest Territories (NWT). Lynx are widespread and cyclically abundant in the North and the lynx harvest is an important source of income for many northern residents. In recent times lynx, along with marten, have provided the principal source of income for northern trappers (Slough et al. 1987).

## Food Habits

Snowshoe hares form most of the diet of lynx across North America. Hares comprise from one-third to nearly all of prey items identified for lynx (for food habits summaries see Quinn and Parker 1987:686; Koehler and Aubry 1994:75; O'Donoghue et al. 1998b). Other common prey items include red squirrels, mice and voles, flying squirrels, ground squirrels, beaver, muskrat, grouse and ptarmigan , and other birds. Ungulates, including deer, caribou, moose, Dall's sheep, and bison, are eaten as carrion and occasionally, excluding bison and moose, as prey (Saunders 1963a; Bergerud 1971; Parker et al. 1983; Stephenson et al. 1991; K. Poole, unpublished). Predation on ungulates is generally restricted to calves, although adults are taken (Stephenson et al. 1991). Use of ungulates appears to be greater during winter and during cyclic low hare abundance. Predation by lynx on red fox and other lynx also occurs, again mostly during periods of low hare numbers (Stephenson et al. 1991; O'Donoghue et al. 1995).

Several trends are evident when examining data on lynx diets. In lynx populations reliant on highly cyclic populations of snowshoe hares, the proportion of hares in the diet generally declines and use of alternative prey increases as hares become scarce (Brand et al. 1976; Stephenson et al. 1991; O'Donoghue et al. 1998b; K. Poole, unpublished). In southwestern Yukon, red squirrels became increasingly important (20-44% biomass) during the years of lowest hare density compared to almost no use (0-4% biomass) during years of high hare densities (O'Donoghue et al. 1998b). Similarly, during years of hare scarcity, use of carrion, red squirrel, ruffed grouse, and other birds increased in central Alberta (Brand et al. 1976), and in southwestern NWT, red squirrels and birds were found more frequently (K. Poole, unpublished data). Red squirrels in particular appear to be an important alternative food source for lynx throughout the North during periods of low hare abundance.

Lynx diets in summer generally have less snowshoe hare and more alternative prey than in winter (Quinn and Parker 1987; Koehler and Aubry 1994). On the Kenai Peninsula in Alaska, Staples (1995) found 64% and 38% hare and 11% and 28% red squirrel in winter and summer lynx scats, respectively. In the Gaspé region of Québec, Fortin and Huot (1995) found hares formed 58% of the diet of lynx during the snow-free period and 85% during winter, with small mammals and red squirrels being important secondary prey during both periods. The lynx diet in southwest Yukon in summer contained a greater diversity of prey, primarily because of the addition of ground squirrels (O'Donoghue et al. 1998c). Other common alternative prey used by lynx during summer include ducks, passerines and other birds, ungulates, and carrion (Saunders 1963a; van Zyll de Jong 1966; Nellis et al. 1972; Brand et al. 1976; Parker et al. 1983). It is unclear whether the greater abundance of alternative prey in lynx diets during summer is a result of decreased hunting success on hares or an increase in the availability of alternative prey.

To our knowledge, differences in diets of lynx by age and sex class have not been reported. At high hare densities, when lynx eat almost solely hares, few inter-class differences in diet would be expected. At lower hare densities, however, some partitioning in resources might be expected. Pulliainen et al. (1995) found no differences in diet between sexes or age categories of European lynx in east Finland where hares dominated the diet. However, in southwest Finland, where hares and white-tailed deer were consumed equally, male lynx consumed more deer and fewer hares than females.

## Foraging Ecology and Hunting Behavior

Due to their heavy dependence on hares for food, morphological adaptations to hunting hares (Murray and Boutin 1991), and almost complete overlap of geographic range with hares (Banfield 1974), lynx are usually considered hare specialists. Accordingly, their foraging behavior is characterized by hunting tactics and movement patterns appropriate for hunting hares.

Lynx hunt by either stalking and rushing at their prey, or ambushing them from "ambush beds" established near the trails of prey (Murray et al. 1995; O'Donoghue et al. 1998a). In the southwest Yukon, the frequency of ambush beds along lynx trails increased nine-fold from the cyclic peak to the low (O'Donoghue et al. 1998a). This corresponded to a switch in diet (*sensu* Murdoch 1969) from hares to red squirrels and the establishment of more ambush beds near squirrel middens. During this period, lynx also initiated progressively more chases of hares from ambush beds (from about 4% to 36% of all chases), although their hunting success was about the same as from stalks for hares, and slightly lower for squirrels (O'Donoghue et al. 1998a). Frequent use of ambush beds by lynx has been noted in one other study (Saunders 1963a, 1963b), but elsewhere lynx seldom ambushed hares (Nellis and Keith 1968; Parker 1981). The costs and benefits of ambushing rather than stalking prey likely depend on prey abundance and behavior as well as the physiological state of the predator (see, for example, Davies 1977 and Formanowicz and Bradley 1987). Ambushing prey when their availability is low may be more energetically efficient for lynx than actively searching for them (O'Donoghue et al. 1998a).

Lynx typically prefer feeding on freshly killed prey over scavenging (Parker 1981; O'Donoghue et al. 1998b). In the southwest Yukon, lynx cached the whole carcasses of only 1.6% of the radio-collared hares they killed, compared to 37.0% of those killed by coyotes (O'Donoghue et al. 1998b). Lynx caches were formed on the surface of the snow by the lynx pulling snow over them. All of the caches that were monitored and retrieved by lynx were consumed in less than two days. Observations of lynx scavenging hares (Nellis and Keith 1968; Parker 1981) and the carcasses of ungulates (see Food Habits) have been made as well, but this appears to occur most often during times of food shortage.

While typically solitary, lynx regularly hunt in mother-kit family groups. Families usually spread out while hunting hares in good habitat, and hares flushed by one animal are often killed by another (Saunders 1963a; Parker 1981; Mowat and Slough 1998; O'Donoghue et al. 1998a). This behavior undoubtedly increases the foraging efficiency of family groups, but likely due to the inexperience of kits, calculated per-individual kill rates of lynx hunting as families were 50-60% lower than those of adults hunting alone (O'Donoghue et al. 1998a). Groups of two or three adult lynx foraging together were recorded in the southwest Yukon during the cyclic decline and low (O'Donoghue et al. 1998a). Very limited data from the latter study suggest that the kill rates of animals in these groups may have been equal to or higher than those of lynx foraging by themselves. Several other authors have recorded small groups of adult lynx together (Carbyn and Patriquin 1983; Poole 1995; Staples 1995; Mowat and Slough 1998), and Barash (1971) recorded adult lynx hunting and feeding together. Aldama and Delibes (1991) recorded similar behavior in Iberian lynx.

## Lynx-Prey Relationships

Although the boreal forest has relatively low species diversity, the food web of boreal vertebrates appears to be more complex than was once recognized (Krebs and Boutin 1998, unpublished). The close relationship between population fluctuations of lynx and snowshoe hares is well documented. Lynx respond both numerically, through changes in their rates of survival, recruitment, and movements, and functionally, through changes in their kill rates, to the hare cycle. The lags in these responses, and in the combined “total response” (which expresses changes in the proportion of the prey population killed relative to prey density), contribute to the cyclic behavior of the system by introducing a delayed density dependent effect (May 1981; Korpimäki and Krebs 1996; Sinclair and Pech 1996).

Numbers of lynx may vary from three to 17-fold during a cyclic fluctuation (Keith et al. 1977; Poole 1994; Slough and Mowat 1996; O’Donoghue et al. 1997). Peak densities are typically reached one year after the cyclic peak for hares, thus the numerical responses of lynx to changing densities of hare show delayed density dependence (Sinclair and Pech 1996; O’Donoghue et al. 1997).

The functional responses of lynx to the hare cycle have only been estimated in two studies. In Alberta, lynx killed about three times as many hares at cyclic peaks as they did when the abundance of hares was low; maximum kill rates were estimated to be about 0.8 hares per day (Keith et al. 1977). Based on their data from snow-tracking, these authors estimated that lynx showed a Type-2 functional response (*sensu* Holling 1959b), or one in which kill rates increase at a monotonically decreasing rate to an asymptotic maximum. Kill rates of hares by lynx varied four to five-fold in the southwest Yukon during a hare cycle, and the estimated maximum kill rates were higher than those in Alberta at about 1.6 hares per day (O’Donoghue et al. 1998b, 1998c). A Type-2 functional response also fit the observed data well for this study. The calculated kill rates in Alberta may have been underestimates, due to the assumptions made that lynx only rested once per day (Brand et al. 1976; Keith et al. 1977), which is questionable (Parker 1981; O’Donoghue et al. 1998b).

Changes in the kill rates of hares by lynx are accompanied by behavioral changes that likely change the "components" (Holling 1959a, 1966) of the functional responses. Lynx chased hares for longer distances when hares were rare than when they were abundant in the southwest Yukon, so "reactive distances" of lynx may have changed as well (O'Donoghue et al. 1998b). The reported success of lynx in catching hares once they had initiated chases has varied from 19% to 57% (Saunders 1963a; Brand et al. 1976; Parker 1981; Major 1989; O'Donoghue et al. 1998b), but it does not seem to be directly related to density of hares (Brand et al. 1976; O'Donoghue et al. 1998b). In the southwest Yukon, the travel rates and total activity time also varied little over the course of the cycle (O'Donoghue et al. 1998b), while activity rates did seem to increase with lower densities of hares densities in the NWT (K. Poole, unpublished). However, switches in prey selection (from hares to red squirrels) and hunting tactics at low hare numbers both likely contributed to the functional responses in the southwest Yukon. Kill rates by lynx and other predators may only decline once hares are concentrated in largely inaccessible habitats, or "refugia" (Wolff 1980; Hik 1995). Refugia for prey species typically act to stabilize predator-prey relationships (Taylor 1984), and a relatively invulnerable subpopulation of hares in very dense cover likely allows them to persist at higher densities through cyclic lows.

The total impact of predation by lynx on the dynamics of hare populations is determined by combining their numerical and functional responses (Solomon 1949; Messier 1995). Based on their calculated responses, Keith et al. (1977) estimated that lynx killed from 2 to 13% of the hares present each winter in Alberta, with peak predation rates occurring two to four years after the hare cyclic high. Likewise, lynx killed an estimated 4 to 32% of hares over winter in the southwest Yukon, with the highest predation rates one to three years after the cyclic peak (O'Donoghue et al. 1998c). Again, the lag in the effect of predation on numbers of hares would contribute to the cyclic dynamics, and throughout the cycle in abundance of hares, lynx are one of the most important predators of hares. Exclusion of lynx and coyotes from experimental areas in the southwest Yukon, when combined with food addition, resulted in densities of hares approximately 11 times higher than those on control areas, and this effect was most pronounced during the cyclic low (Krebs et al. 1995; Krebs and Boutin 1998).

While the effects of predation by lynx on hares may be considerable, lynx likely have little impact on other alternative prey in the boreal forest. Grouse were the main alternative prey of lynx in Alberta (Brand et al. 1976), but they never represented more than an estimated 12% of the total biomass in the diets of lynx. Keith et al. (1977) attributed synchronous fluctuations in numbers of grouse and hares to changes in predation rates on grouse by raptors. In the southwest Yukon, red squirrels were the most important alternative prey for lynx during years of low abundance of hares (O'Donoghue et al. 1998b). However, even when squirrels represented 79% of kills by lynx during winter, the total impact of predation by lynx was less than 4% of the estimated population of squirrels (O'Donoghue et al. 1998c). The negligible impact of predation by all terrestrial predators on red squirrels was also confirmed experimentally in the Yukon (Stuart-Smith and Boutin 1995). Throughout their range, lynx appear unable to persist at high densities when numbers of snowshoe hares are low. This both limits the effect of their predation on alternative prey, and allows numbers of hares to recover from cyclic lows.

## Habitat Selection and Use

At the largest spatial scale, lynx occupy the boreal, subboreal and western montane forests of North America (McCord and Cardoza 1982; Quinn and Parker 1987). They occur in many forest types that are not truly boreal, although all of the forests they occupy are relatively simple in terms of physical structure and species composition (Koehler and Aubry 1994). Lynx are absent or uncommon in the wet coastal forests of western Canada and Alaska. Lynx are more or less ubiquitous residents of northern forests, with their distribution becoming more discontinuous toward the south. Legendre et al. (1978) demonstrated that lynx were most abundant in the boreal forest of their northeast Québec study area, and that lynx distribution was associated with the distribution of the hare. Lynx were also found in the sub-arctic forest, which was dominated by balsam fir and paper birch. Lynx were not found in the more open subarctic forests and tundra to the north. Dwyer et al. (1989) concluded that lynx in central Ontario were primarily associated with upland boreal forest and, to a lesser extent, marshlands with black spruce, alder and willow. Lynx avoided wetlands with cattails, oak, maple, and hemlock. Quinn and Thompson (1987) found that lynx were abundant in both the boreal and mixed-wood boreal zones in central Ontario; these authors compared several population parameters among the two zones and found no strong indication to suggest differences in fitness or density. In western Canada, Hatler (1988) reported that the majority of the lynx harvest in British Columbia (B.C.) came from the only area of true boreal forest in the province.

At the stand level, lynx prefer regenerating forest stands like those of its main prey, the snowshoe hare (Thompson 1988; Koehler and Aubry 1994). Throughout the north, lynx select older regenerating stands (greater than about 20 years of age) both of human and fire origin at all points in the hare cycle (Kesterson 1988; Thompson et al. 1989; Major 1989; Perham 1995; Staples 1995). Lynx do not frequently use younger regenerating stands (Thompson et al. 1989; Golden 1993; Perham 1995; Staples 1995). It appears climax shrub stands are also avoided (Staples 1995), even when they contain sizeable hare populations (Murray et al. 1994), although the work of Major (1989) suggests these stands may receive greater use in summer. Many authors have demonstrated use (though not selection) of mature forest stands, and indeed one study team (Murray et al. 1994 and O'Donoghue et al. 1998a) worked where all forested stands were mature. It is interesting to note that these authors reported a persistent lynx population in this area, even during a cyclic population low (O'Donoghue et al. 1997). Kesterson (1988) and Staples (1995) both demonstrated strong selection for mature stands included within a mid-seral burn, but they demonstrated strong selection against mature forest when it was the matrix habitat. We conclude that mature coniferous habitat can support lynx in the North, although the quality of mature habitat may vary regionally. Major (1989) and Mowat et al. (1998, unpublished) demonstrated that mature aspen, white spruce, and black spruce stands in three areas of Yukon contained significant quantities of browse and horizontal cover, and contained modest numbers of hares during all phases of the cycle.

Do lynx and hares show similar patterns of habitat selection? We suggest yes, with two exceptions. First, hares appear to select more dense stands than lynx (O'Donoghue et al. 1998a). Presumably lynx are unable to hunt in the densest stands and are hence excluded. This suggestion is consistent with the observations of many researchers (e.g., Wolff 1980) that hares survive in pockets of dense habitat during the cyclic low. Second, hares appear to select dense shrubs with little aerial cover, at least during periods of reasonable abundance, whereas lynx rarely use such stands. Keith (1990) suggested that hares need dense understory cover but that "overstory characteristics are of doubtful significance in habitat selection." It is unclear, however, whether lynx avoid some shrub stands because they lack aerial cover or because they are simply too dense to hunt in successfully. Based on observations of hares using denser cover than lynx in forested stands, we suggest that the latter explanation is correct.

Only one study has measured lynx and hare habitat use over the course of a cyclic fluctuation (O'Donoghue et al. 1998a). In the southwest Yukon study, the pattern of habitat selection by lynx roughly followed that of hares though, on average, hares used denser stands in all years. Lynx and hares used habitats with the densest vegetative cover during the cyclic decline, while both used more open habitats when hares were abundant (O'Donoghue et al. 1998a). This study was conducted in a mature forest matrix and it is unclear whether lynx also move to denser habitats in regenerating stands when hares are scarce. Within years, lynx may demonstrate broader habitat choice during summer when alternative foods are more abundant (Major 1989; Fortin and Huot 1995).

Kesterson (1988) and Staples (1995) both demonstrated selection for a relatively rare habitat, which they describe as mature stands within a burned forest matrix. Both these authors suggested that lynx tend to hunt along the edge of this habitat. Major (1989) also suggested that lynx hunted edge habitats—in this case, the edge of dense riparian willow stands. The use of habitat edges may be an important hunting strategy for lynx, which may allow them to hunt hares that live in habitats that are normally too dense to hunt effectively. Several authors have shown that lynx select against openings such as water or open meadows, although some use of terrestrial openings was always detected (Murray et al. 1994; Fortin and Huot 1995; Poole et al. 1996). Most openings have few if any resident hares, so this result is not surprising, especially in winter. This does not indicate that lynx will not cross openings; indeed the fact that lynx were occasionally located in openings, including farmland (Fortin and Huot 1995), suggests they are not against entering them. We found lynx regularly crossed several hundred meter wide openings during our work in NWT and Yukon; occasionally, lynx crossed frozen lakes and rivers >1 km across (K. Poole and G. Mowat, personal observation).

While relatively few lynx dens have been described in the North, all had similar structural aspects regardless of their stand types. Berrie (1974) described three dens located in central Alaska; two were in tangles of spruce blowdown, and the other was in a tangle of spruce roots washed up on the bank of a creek. Stephenson (1986) located one den site in a mature spruce-birch stand, with the den located in an area of numerous deadfall trees. Kesterson (1988) stated that “lynx seemed to select den sites in or near mature habitats dominated by large quantities of wind-felled trees.” Hatler (1988) described a den found in logging debris and blowdown on the edge of a six to eight-year-old cut-block in northern B.C. Slough (in press) located 39 lynx dens in south-central Yukon. One of these den sites was in a mature spruce stand, one was in a mature subalpine fir stand, and 37 were in regenerating stands about 30 years in age. Three dens were under young, bushy subalpine fir trees, two were in dense copses of mature willow, and 34 were under blowdown, usually dense tangles of trees. Poole (1992) located five lynx den sites in southwestern NWT. Den sites were characterized as areas of moderate to heavy deadfall located in mature conifer or regenerating mixed conifer and deciduous stands. In summary, female lynx appear to select den sites in a number of forest types in the North. Lynx do not appear constrained to select specific stand types; rather, the feature that was consistently chosen was the structure at the site itself. Wind-felled trees were the most common form of protection selected by female lynx, although other structures such as roots and dense live vegetation were also used. The importance of proximity to areas with high prey density to den site selection has not been examined.

Wildfire, which is the most important factor in the dynamics of the northern boreal forest ecosystem (Kelsall et al. 1977; Viereck 1983), is a major habitat modifier (Johnson et al. 1995). Johnson et al. (1995) and Paragi et al. (1997) suggest that optimum habitat for hare and lynx can be achieved in interior Alaska by frequent and numerous but relatively small fires, or large patchy fires with abundant unburned inclusions. However, the effects of spatial heterogeneity and juxtaposition of habitats on behavior and population dynamics of lynx are unstudied.

Logging, which is also an important factor in the dynamics of many boreal forests, restarts the succession necessary to create optimum hare and lynx habitat, but often removes the structure needed for denning by lynx. Whether the regrowth on a logged area becomes usable hare habitat will depend on site level factors and silviculture treatment post-harvest (Thompson 1988; Koehler and Brittell 1990). Thompson (1988) suggested that planted and tended boreal sites are used less by hares and lynx than naturally regenerating sites. Thompson (1988) further suggested that increased hare and lynx populations would occur with logging plans that incorporate numerous small stands of mature forest, hence increasing the amount of uncut forest-successional edge. There may be a limit to the benefit of edges for hares because predation on hares may increase in small habitat patches (Chapter 6); very small patches may present predation risks that are not sustainable for hares. We conclude that logging will only provide quality lynx habitat if a dense understory of coniferous or deciduous vegetation results. Because hares select habitat based more on understory cover than browse (Chapter 6), plant species appear to be of secondary importance. Except for extremely dense stands, silvicultural prescriptions such as precommercial thinning or herbicide application that thin or remove the understory probably reduce habitat quality for lynx (but see Sullivan 1994, 1996). Leaving groups of standing and downed trees may allow for denning opportunities within the cutting area and not force female lynx to search out den sites in mature forest, as suggested by Koehler and Brittell (1990). Denning structure must be scattered about the landscape because female lynx probably establish temporary dens throughout their home range during the period when kittens are old enough to travel but not hunt (Bailey 1981). Several of the above authors have suggested that good lynx habitat includes both late and early seral components; we conclude that lynx can survive in single habitat types, such as early seral or mature forests, as long as the features to support both hares and denning by lynx exist.

## Spatial Organization, Social Behavior

The lynx spacing mechanism is functionally similar to that of other Carnivora such as mustelids and ursids. Brittell et al. (1989) suggested that lynx have a social organization similar to that of bobcats and cougars, consisting of social intolerance and mutual avoidance (Seidensticker et al. 1973; Bailey 1974). Powell (1979) described this land tenure system as "intrasexual territories" and Kesterson (1988) also used this description for lynx. In this system, resident individuals maintain intra-sexually exclusive territories, and males may or may not have larger home ranges than females. Lynx are territorial, but not according to the strictest definitions (see Hornocker et al. 1983 for a related discussion of this topic). Scent-marking using feces, sprayed urine, or anal secretions may be used to mark home ranges and to provide both spatial and temporal information that may reduce confrontations (Saunders 1963b; Mellen 1993; Staples 1995). Lynx also show strong range fidelity, often over many years (Poole 1995; O'Donoghue et al. 1998c), have core range areas that seldom overlap (Poole 1995; O'Donoghue et al. 1998c), and appear to avoid contact among individuals (Poole 1995) and violent encounters (Poole 1995; Mowat and Slough 1998). Poole's (1995) work suggests that some sort of spacing mechanism was operating to keep same-sex animals separated in time and space. However, the tendency toward neutral indices of dynamic interactions (the degree to which two animals avoid, ignore, or attract each other [Macdonald et al. 1980]) indicated little or no active avoidance or overt defense of areas between overlapping or adjacent pairs, suggesting that this spacing was upheld by relatively passive means. Conflict among individuals is rare in lynx (Poole 1995; Mowat and Slough 1998) and perhaps in other solitary felids as well (Hornocker and Bailey 1986). Aggressive lynx-lynx encounters do occur, however, and occasionally result in cannibalism, primarily during years of food shortage (Poole 1994; O'Donoghue et al. 1995; Mowat and Slough 1998).

Lynx home range sizes vary among areas, sexes, seasons, and cyclical phases. It is difficult to compare home range sizes among studies because of differing methods of data collection, sample sizes, and analysis techniques. Many studies did not determine the ages of the individuals tracked and could not identify subadults. Further, the home range size of breeding lynx may increase (Kesterson 1988), hence yearly home ranges may vary depending on when the data were collected, especially when sample sizes are small.

Koehler and Aubry (1994) summarized home range sizes for lynx. Dramatic variation in home range size has been reported for lynx across their North American range (8-738 km$^2$), not all of which can be explained by differences in measurement and analysis techniques. Male home range sizes are usually larger than female ranges (Kesterson 1988; Koehler and Aubry 1994; Fortin and Huot 1995; Perham 1995; Slough and Mowat 1996; O'Donoghue et al. 1998c, but see Ward and Krebs 1985 and Poole 1994). In the south-central Yukon, yearling lynx had similar home range sizes to adults (Slough and Mowat 1996), while Noiseux and Doucet (1987) found that yearling home ranges were generally smaller than adult home ranges in southern Québec. Philopatry to home ranges has been reported among individuals of both sexes resident over several years, but home range shifts and abandonment are also common (Breitenmoser et al. 1993b; Poole 1994; Perham 1995; Slough and Mowat 1996; O'Donoghue et al. 1998c).

Poole (1994), Slough and Mowat (1996), and O'Donoghue et al. (1998c) showed that lynx range size increased dramatically after the sudden decrease in hare abundance in the North. Perham (1995) studied lynx after a hare decrease in Alaska and found great variation in home range size of males, several of which had ranges >200 km$^2$. Poole (1994) and Slough and Mowat (1996) presented data for several years before the hare decrease and home range size changed little during this period. Ward and Krebs (1985) suggested lynx home range size changed with hare abundance; however, they used a categorical analysis (with three categories of hare abundance) to test this relationship, and only the largest and the smallest categories differed significantly from one another ($p < 0.05$). Therefore, their data could also be interpreted to show similar home range sizes through the lynx cycle followed by an increase after the sudden hare population decrease. The only researchers to empirically test for a linear relationship between lynx home range size and hare abundance were Brand et al. (1976) and Slough and Mowat (1996). Brand et al. (1976) used only eight home range sizes across five different winters and were further forced to pool the sexes for their analysis; these limitations aside, they did not find a linear relationship between lynx home range size and hare abundance. Slough and Mowat (1996) had larger sample sizes across eight years and found no liner relationship for either sex.

It may be more appropriate to test lynx home range size against hare abundance the previous year because there appears to be a one year lag in the numeric response of lynx to hares (Krebs et al. 1995; O'Donoghue et al. 1997). We used correlation analysis and published data from Poole (1994) and Slough and Mowat (1996) to test for a linear relationship between lynx home range size and hare density the previous year. We used mean yearly home range sizes for each sex because of the large variation in sample size among years ($n$ = 1-15 individuals per year). These conservative tests suggest there was no linear relationship between lynx home range size and hare density the previous year for both sexes and study areas ($p > 0.3$, df 3-7 in all cases; Fig. 9.1a,b).

Lynx did increase their home range sizes dramatically following the hare crash, and as mentioned above, it would further appear that home range size changes relatively little during years of high hare abundance. There appears to be a threshold hare density below which lynx home range size increases (Fig. 9.1a,b). We did not compare yearly changes in home range size for individual lynx; perhaps some individuals do alter their home range size with hare abundance in a more linear fashion.

Home ranges vary seasonally in lynx. Females hunt alone while the kittens are young, making solitary forays from the den site. As kittens get older they begin to travel with the female, although it is assumed they are cached at temporary den sites when she is hunting (Kesterson 1988), as has been recorded for bobcats (Bailey 1979). Kesterson (1988) and Mowat and Slough (1998) observed that female home ranges were very small during the denning period; range size increased appreciably in mid-summer once the kittens were large enough to begin leaving the den site. By early fall, female home range size expands to reoccupy the area used before birth, and we assume that the kittens travel with the female, even while hunting (Bailey 1979; Winegarner and Winegarner 1982; Kesterson 1988). Kittens remain with the mother throughout the winter. Family groups begin to break-up in early March (Saunders 1963b; Brand et al. 1976; Parker et al. 1983; Poole 1995; Mowat et al. 1996b). Kittens appear to be closely associated with their

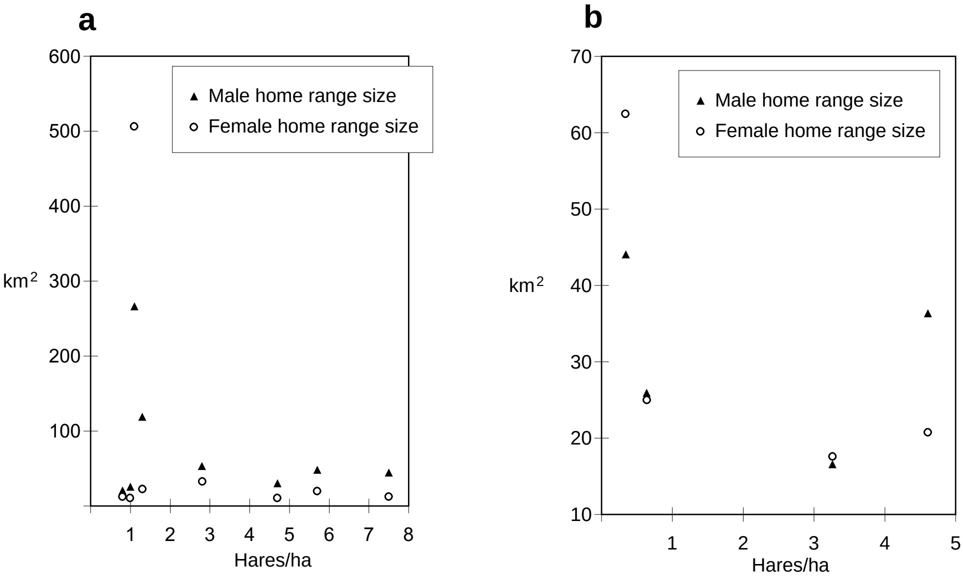

**Figure 9.1**—The relationship between lynx home range size (*n* = 1-15) and hare density the previous year across: (a) eight years of a hare cycle in south-central Yukon (Slough and Mowat 1996), and (b) four years of a hare cycle in southwest NWT (Poole 1994; K. Poole, unpublished).

mothers until February or early March, when the association weakens; natal dispersal begins in late April and early May (Poole 1995; Mowat et al. 1996b). Some juvenile kittens disperse immediately (Poole 1995; Slough and Mowat 1996), while others remain in the natal area for up to one year after their first winter (Kesterson 1988; Slough and Mowat 1996). Similar behavior has been recorded for bobcats (McCord and Cardoza 1982) and Iberian lynx (Aldama and Delibes 1991). Dispersal from the mother's home range can be sudden or it can be a more gradual process (Kesterson 1988; Poole 1994; Mowat and Slough 1998). Separation of the kittens and mother may be hastened by the subsequent breeding of the adult female (McCord and Cardoza 1982); however, Mowat and Slough (1998) documented a female and male lynx together for several days in the company of the female's 10-month-old kittens. Kesterson (1988) noted no strong trend toward increased home range size of males during the breeding season in his study population, though a few individuals did appear to increase their range size while breeding.

Home range overlap is often used to assess social patterns in mammals. This parameter is probably measured even more inaccurately than home range size because it is affected by all the constraints mentioned above for home range and is further complicated by the fact that errors can be made during interpretation of the measurement when relatedness of individuals is unknown. Unfortunately, relatedness of individuals is rarely known in field studies. Given the above constraints, it is not surprising great variation in overlap has been shown for both sexes (Ward and Krebs 1985). In the NWT, Poole (1995) recorded variable amounts of overlap among lynx during peak and declining densities of snowshoe hares. Much of the overlap was among females and was attributed to several pairs of females that showed large overlap in home range, often for several years. These females were assumed to have been related. This observation shows the weakness in measuring range overlap when individual relationships are unknown. Researchers working on other species of lynx have also recorded variable home range overlap within sexes (Breitenmoser et al. 1993a; Jedrzejewski et al. 1996; Ferreras et al. 1997). Generally, male and female home ranges overlap completely while within-sex overlap is usually modest or may be confined to one or two pairs of individuals per study (e.g., Poole 1995). Home range exclusiveness may be a function of degree; some overlap may occur at the 90 or 95% home range contour level, but, as noted in Poole (1995), little may occur among the 50% contour core areas.

Felids are said to have a social system based on matrilineal descent (Kleiman and Eisenberg 1973; Kerby and Macdonald 1988). This theory would suggest that pair bonds between females, either mother-daughter or sibling pairs, persist and that these relationships form the basis for the organization of social structure. This theory is difficult to test in solitary species, but there is evidence suggesting that female pair bonds do persist in Canada lynx and other lynx. Female kittens sometimes establish home ranges within those of their mothers (Kesterson 1988; Breitenmoser et al. 1993b; Slough and Mowat 1996). Kesterson (1988) found that three female kittens remained in or near their natal ranges during the entire period for which they were monitored. This trend has been noted in other solitary felids (Eisenberg 1981; Sundquist 1981; Ross and Jalkotzy 1992) and suggested by Poole (1994) and Staples (1995) for Canada lynx. Secondly, adult females may retain amicable contact with their female offspring throughout their life. Barash (1971) witnessed a group of two adult and one yearling lynx hunt and share a ground squirrel. Carbyn and Patriquin (1983) located two different female and kit groups together five times over a 30-day period. Staples (1995) recorded two different adult females together, each with a single yearling female offspring, a total of 15 times. O'Donoghue et al. (1998a) witnessed several adult animals hunting together through three winters during the cyclic hare decline and low. Mowat and Slough (1998) often recorded related adult females together during their study of lynx in south-central Yukon, even when both females had accompanying kittens. Mowat and Slough (1998) also reported an incident where an adult female and her yearling offspring gave birth within 800 m of each other. Both Poole (1995) and O'Donoghue et al. (1997) found female home ranges with large overlap, although this was not the norm on either study area; both groups felt that these females were likely related.

The persistence of female bonds has important implications for lynx conservation. Matrilineal groups may confer greater fitness on their members by allowing group hunting at certain times (O'Donoghue et al. 1998a), the possibility of adoption of orphaned kittens (Carbyn and Patriquin 1983; Mowat and Slough 1998), and a reduction in the investment in territorial defense. In addition, populations with related individuals may attain higher density because territoriality may be relaxed among relatives.

## Behavioral Responses of Lynx to Humans

Staples (1995) presented data on lynx responses to close encounters with humans. As suggested by earlier authors, he found that lynx were generally tolerant of humans. The work of Staples (1995) and other anecdotal accounts of lynx behavior suggests that lynx can tolerate human disturbance and even continued presence. Trappers will relate that lynx are relatively easy to capture; they appear to have little fear of human scent, they respond to baits and lures, and can be attracted using visual attractants.

Humans may exert potentially negative influences on lynx by building residences and roads in and through lynx habitat, by altering and modifying existing habitats, and by direct disturbance through recreation or travel in areas inhabited by lynx. Our anecdotal experiences suggest that lynx will tolerate moderate levels of snowmobile traffic through their home ranges. We could not detect changes in lynx movement patterns or home range in our northern studies despite constant, repetitive and daily travelling through the study areas to check traps and locate animals. Lynx appeared to readily cross highways, and several animals in southwestern NWT established home ranges adjacent to roads. Lynx are also regularly sighted sitting along roadsides in the North. Lynx tracks were regularly observed adjacent to residential areas in both Yukon and NWT, although we do not know if these animals were residents. Lynx may tend to avoid areas with higher levels of disturbance or greater fragmentation of habitat from development, although this has not been rigorously tested. Several studies of lynx have occurred in areas with reasonably dense rural human populations and interspersed agricultural areas, which further suggests lynx can tolerate daily human use and presence in an area (Brand and Keith 1979; Fortin and Huot 1995). Both these studies demonstrated resident lynx populations of about 10/100 $km^2$.

Although lynx will generally flee when closely approached, they appear to become bolder and less wary of people during periods of low prey abundance. Anecdotal observations include a lynx eyeing a dog on the edge of a mid-summer wedding celebration in the NWT, another killing a dog outside a trapline cabin while the trapper was present, and a third defending a fox caught in a trap while the trapper approached. Several incidences of lynx stalking domestic animals throughout the Yukon during low prey abundance have been recorded (Mowat and Slough 1998).

## Population Dynamics

Lynx numbers fluctuate in response to population levels of snowshoe hare, and the decline in lynx numbers generally lags one year behind the decline in hare numbers (Elton and Nicholson 1942; Butler 1953; Keith 1963; Brand and Keith 1979; Boutin et al. 1995). Lynx populations, as indexed by harvest data, (Fig. 9.2) fluctuate in synchrony over vast geographic areas, showing roughly similar trends in timing and amplitude of cyclic peaks and lows across the continent (Ranta et al. 1997). The lynx cycle appears to initiate and emanate from central Canada, following similar trends in the hare cycle (Smith 1983), such that peak lynx harvests in Saskatchewan and Manitoba from 1960 to 1980 occurred around the turn of the decade, and two to four years later in Yukon, Alaska, and Québec. Long-distance dispersal of

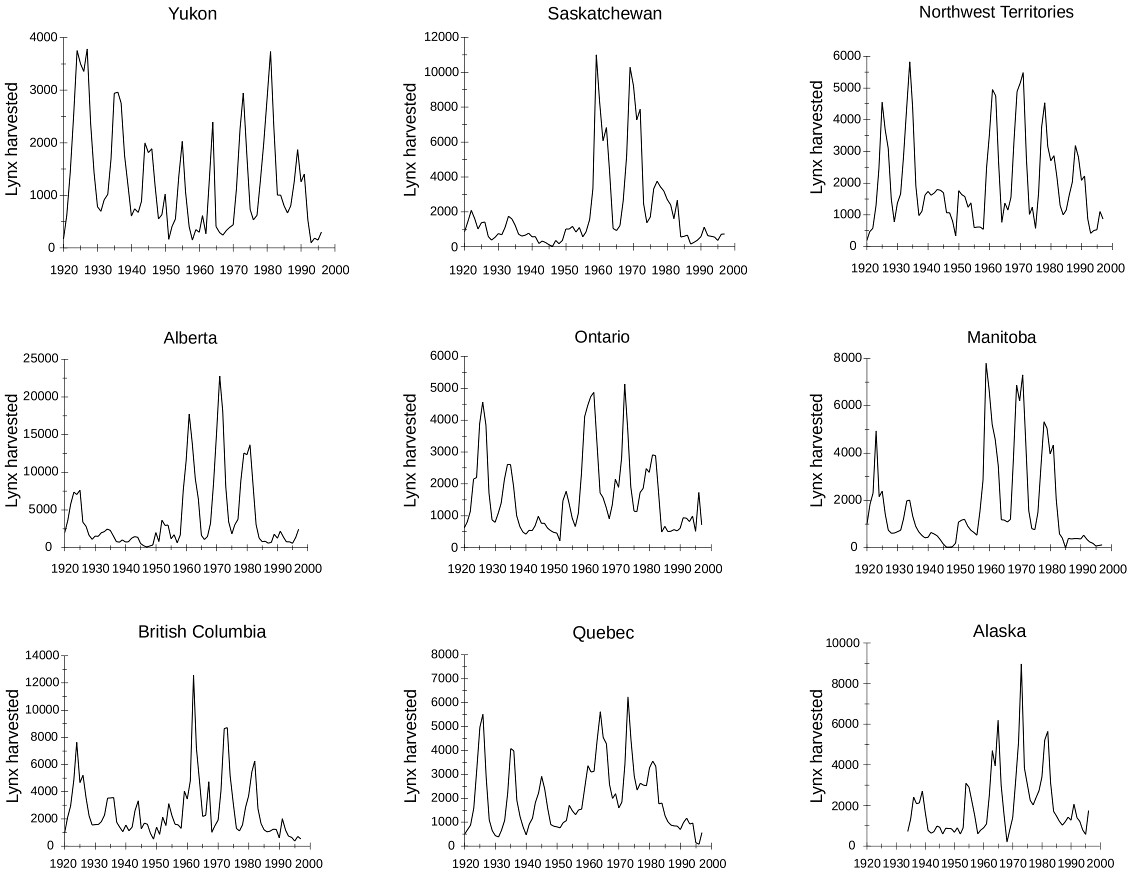

**Figure 9.2**—Lynx harvest from 1920 to 1997 for eight Canadian territories and provinces and Alaska. Data from 1920 to 1983 were primarily from Novak et al. (1987). Data from 1984 to 1997 were obtained from the individual provinces and territories and from the State of Alaska.

lynx and other predators during cyclic declines could act as a synchronizing element of the hare cycle (Butler 1953; Lack 1954; Korpimäki and Krebs 1996). In a recent analysis of time series data for hare and lynx, Stenseth et al. (1997) suggest that the dominant community linkages are three dimensional for the hare cycles, and two dimensional for the lynx cycles. The hare appears to be regulated from below and above (thus both the vegetation-hare and hare-predator interactions must be considered to understand hare dynamics), whereas the lynx seems to be regulated only from below (thus, for the lynx, the hare-lynx interaction dominates). This lack of a third dimension suggests that lynx social structure is not a major factor limiting lynx population growth.

Akçakaya (1992) built a mathematical prey-predator model such that trophic functions are modeled as functions of prey-to-predator ratios rather than as functions of prey density only (functions of per capita resources). This model developed limit cycles consistent with changes in a south to north gradient and predicted a periodicity of around 10 years. Both of these patterns are consistent with the true dynamics of the cycle. This paper demonstrates the need to consider both lynx and hare population size when considering lynx population dynamics.

The cycle in lynx and hare numbers is often broken into phases. The low period typically lasts three to five years and is denoted by low population density and a mild decline and recovery in numbers through the period (Poole 1994; Slough and Mowat 1996; O'Donoghue et al. 1997). During the increase phase, about three years in duration, lynx numbers increase quickly (Poole 1994; Slough and Mowat 1996; O'Donoghue et al. 1997). The peak phase is usually a two-year period of high lynx density with modest or no population growth (Poole 1994; Slough and Mowat 1996; O'Donoghue et al. 1997). The decline or crash phase of the hare cycle is one to two years in duration; lynx numbers decline dramatically during this phase of the cycle.

Quinn and Parker (1987) and Koehler and Aubry (1994) have summarized lynx densities. More recent work suggests that peak densities in lightly or unharvested areas in the North may range between 30-45 lynx/100 km$^2$ in recent burns (Poole 1994; Slough and Mowat 1996). Peak densities in a mature forest matrix in the North or in the more southern part of the lynx's range are typically lower, at 8-20 lynx/100 km$^2$ (Parker et al. 1983; Banville 1986; Kesterson 1988; Noiseux and Doucet 1987; Fortin and Huot 1995; O'Donoghue et al. 1997). Brand et al. (1976) estimated 10 lynx/100 km$^2$ during a hare peak in central Alberta in a mixed forest matrix with inclusions of agriculture. Population densities during the low are typically less than 3 lynx/100 km$^2$, regardless of habitat quality (Brand et al. 1976; Poole 1994; Staples 1995; Slough and Mowat 1996; O'Donoghue et al. 1997). In south-central Yukon, Slough and Mowat (1996) calculated a finite rate of increase ($\lambda$) of 2.03 to the peak, stable numbers during the first year of declining hare populations ($\lambda = 1.01$), and $\lambda = 0.01$ during the decline. It should be noted that all densities presented here are rough figures, and although they are adequate to demonstrate general temporal and spatial trends, they combine several different methods, none of which are based on a sampling methodology or present confidence intervals.

As may be expected, age structure changes with population size in lynx. Lynx populations are dominated by young animals during the late increase, peak, and early decline phases of the cycle, leaving an aging adult cohort through the low phase (Nellis et al. 1972; Brand et al. 1976; Poole 1994; Slough and Mowat 1996; O'Donoghue et al. 1997). Average age increases through the low phase due to lack of recruitment, and the oldest age structure is in the first part of the increase phase, before new recruits are added (Slough and Mowat 1996). There is less evidence for cyclic variation in sex ratios. Sex ratios of kittens do not differ from equality (Poole 1994; Slough and Mowat 1996). Sex ratios of adults and yearlings did not differ from unity in any year in south-central Yukon (Slough and Mowat 1996), but in southwestern NWT there appeared to be a shift in sex ratio from greater numbers of males at peak population levels to more females during low levels (Poole 1994). Lembeck (1986) also documented a shift from predominantly males to more females in an unharvested bobcat population during a population decrease, and suggested this resulted from a population control mechanism linked to females. Smaller individuals may be better able to survive under conditions of low food abundance, hence the shift to a population composed of more females during low levels. Trapping also tends to remove males in greater proportion to their abundance because they have larger home ranges and may disperse more often.

Most lynx harvests are biased toward males (Berrie 1974; Quinn and Thompson 1987), but even sex ratios (Brand and Keith 1979) or proportionately more females (Bailey et al. 1986) have been observed. The observation of more females in the harvest by Bailey et al. (1986) was coupled with a harvest that exceeded replacement. Age structure of untrapped populations would presumably be composed of older-aged animals compared to harvested populations (Knick 1990; Poole 1994; Slough and Mowat 1996). Harvests of lynx in the area surrounding an untrapped study area in south-central Yukon had 36% fewer kits, 40% more yearlings, and 4% fewer adults than were present on the study area (Slough and Mowat 1996). Yearlings were greatly over-represented and kits under-represented in the harvest, as suggested in other areas (Brand and Keith 1979; Quinn and Thompson 1985).

Lynx dispersal, immigration, survival, and recruitment are closely linked throughout the snowshoe hare cycle. Population growth in lynx is a result of a high percentage of breeding females, large litters, high kit survival, low mortality, and immigration rates that balance or even exceeded losses to emigration. The lynx population decline is due to increased dispersal, high natural mortality, and a collapse in recruitment and immigration. In lynx studies in southwestern Yukon and southwestern NWT, all collared lynx resident prior to or during the decline in hare abundance dispersed or died by the end of the first winter of low hare densities (Poole 1994, 1997; O'Donoghue et al. 1995, 1997). In south-central Yukon, only two previously resident lynx remained after the hare decline from a population peak of over 130 animals (including residents, non-residents and all age classes; Slough and Mowat 1996).

## Recruitment

Canada lynx breed through March and April in the North (Quinn and Parker 1987). Breeding pairs may remain together for several days (Poole 1994; Mowat and Slough 1998) and it is assumed females only breed with one male, but this assumption has not been tested (McCord and Cardoza 1982). It is unclear whether female lynx are induced or spontaneous ovulators (Quinn and Parker 1987). Gestation is approximately 70 days (Crowe 1975; Quinn and Parker 1987). In south-central Yukon, the mean date of birth for litters to adult females was 26 May (range 12 May-7 June) and did not differ among years (Mowat et al. 1996b; Slough and Mowat 1996). In southwestern NWT, date of birth appeared to be predominantly in the last 10-12 days of May (K. G. Poole 1992, unpublished). Kittens are born altricial; their eyes open at 10-14 days of age, though their vision is significantly impaired by large cataracts for several weeks thereafter (McCord and Cardoza 1982; G. Mowat, personal observation). Den sites are usually surface scrapes; the female usually scrapes back the ground cover and places the kittens on dry ground (Mowat 1993; Slough, in press).

During the period when hares are most abundant, yearling lynx give birth (Brand and Keith 1979; Quinn and Thompson 1987; Slough and Mowat 1996). In one study, yearling females gave birth approximately two to three weeks later than adults (Mowat et al. 1996b; Slough and Mowat 1996). Male lynx are thought to be incapable of breeding in their first year (McCord and Cardoza 1982; Quinn and Parker 1987).

During the cyclic hare low, lynx pregnancy rates vary from 0 to 100% (see review in Koehler and Aubry 1994), but sample sizes are often very small during this period, hence estimates tend to be unreliable. Adult in utero litter size averages three to four during the low period (Brand and Keith 1979; O'Connor 1984; Slough and Mowat 1996). Birth rate, the proportion of females that give birth, has been measured twice during the first year of the low phase and Poole (1994) and Slough and Mowat (1996) suggested, on the basis of few observations, that live births were few or nonexistent. Few yearling females conceive during the low phase (Brand and Keith 1979; O'Connor 1984), and Mowat et al. (1996b) argued that few or no yearlings successfully give birth. All studies report no kittens present during the second winter following the hare crash (Brand et al. 1976; Poole 1994; Slough and Mowat 1996; O'Donoghue et al. 1997); the few kittens born generally have little chance of survival. However, kittens have been reported throughout the cycle in the Klondike Valley in southwestern Yukon (J. Fraser, personal communication) and in the Mackenzie River Delta in northwestern NWT (K. Poole, unpublished); these exceptions may point to areas of optimum hare and lynx habitat. It is unclear how long the period of no or low recruitment continues; many authors have argued that recruitment fails for three to five years (Brand and Keith 1979; Parker et al. 1983; Mowat et al. 1996b). In southwestern NWT, no kittens were present among collected carcasses ($n = 69$) during the two years following the hare decline (Poole 1994). In south-central Yukon, Slough and Mowat (1996) found no kittens in a sample of seven carcasses during the first year of low hare numbers; however, Slough (1996) analyzed pelts ($n = 45$) collected from a broader area for the same year and found 13% kittens. Slough (1996) believed that this overestimate was caused by a decline in lynx body size (and hence pelt length) during the crash.

Female lynx may begin to give birth before hare densities start to increase. Brand et al. (1976) saw live litters in summer during two different years of the cyclic low in hare abundance in central Alberta. Slough and Mowat (1996) found that three females gave birth to litters during the latter part of the low phase on their study area. The authors suggested that two other females may have done so as well. Perhaps the most convincing evidence of recruitment during the latter part of the low phase comes from the analysis of trapper samples. Slough and Mowat (1996) found 13 ($n = 33$) and 25% ($n = 29$) kittens in a carcass collection during the last two years of low hare and lynx densities before the hare increase. Clearly, some young lynx are recruited to the trappable population during the hare low, especially in the latter years of the low (Slough and Mowat 1996).

As hare numbers increase, yearling females begin to breed and adult litter sizes increase (Brand and Keith 1979; O'Connor 1984; Slough and Mowat 1996). Pregnancy and birth rates range from 73 to 100% for adults and 33 to 100% for yearlings during this period (Poole 1994; Mowat et al. 1996b; and see Table 3 in Mowat et al. 1996a:438). Adult litter size averages four to five during periods of hare abundance (Mowat et al. 1996a:438). Kitten survival is high (50-83%) during the increase and peak phase of hare cycle (Brand et al. 1976; Poole 1994; Slough and Mowat 1996). However, survival of kittens of yearling mothers was low (<26%) even in high quality habitat at all times of the hare cycle in south-central Yukon (Mowat et al. 1996b; Slough and Mowat 1996). These authors suggest yearlings contribute little to recruitment but the generality of this pattern is unclear. Lynx have large litters in comparison to other carnivores of their size (Mowat et al. 1996b) and this, combined with high kitten survival, generates rapid population growth during the increase and peak phases of the cycle (Slough and Mowat 1996).

The birth rate of adults and yearlings is reduced the spring following the hare decline (Poole 1994; Slough and Mowat 1996). Kitten survival also declines to near zero the year after hare numbers crash (Brand et al. 1976; Parker et al. 1983; Poole 1994); this decline was delayed one year in south-central Yukon (Slough and Mowat 1996). Here, most adult females gave birth to large litters while densities of hares were declining precipitously, but their birth rate declined to zero one year after the hare crash (Slough and Mowat 1996). In utero pregnancy rates and litter sizes declined little during the first year of the lynx crash and continued to overestimate reproduction and recruitment during the decline and low (Mowat et al. 1996a), making these measurements weak estimators of recruitment and poor predictors of the lynx decline.

In summary, lynx reproduction is closely tied to hare abundance in northern populations. Kitten survival declines to zero shortly after the hare crash, although some lynx continue to breed and possibly give birth for one more year (Poole 1994; Mowat and Slough 1998). Conception by adults continues through the low phase but very few live litters are born, especially during the two years following the lynx decline. In utero litter size declines through the low, which results in lower litter sizes early in the increase phase. Lynx may begin to recruit juveniles at least two years before appreciable recovery in hare numbers. We suggest the perception that lynx recruitment is zero during hare lows is overstated, at least in the far North. Northern lynx populations do recruit some individuals when hares are scarce and these individuals may be important in maintaining lynx populations through a hare low phase.

## Mortality and Survival

Survival rates of lynx vary tremendously as snowshoe hare abundance changes through the cycle. Not surprisingly, the level of trapping in and around the population under study influences survival rates. Annual survival rates of adults during the increase and peak phase of the hare cycle were >0.70 in a lightly trapped population in southwestern Yukon

(O'Donoghue et al. 1997), and >0.89 in largely untrapped populations in southwestern NWT and south-central Yukon (Poole 1994; Slough and Mowat 1996). Annual survival rates of adult lynx remained high (0.78-0.95) (Poole 1994; Slough and Mowat 1996) or declined slightly (0.45-0.63) (O'Donoghue et al. 1997) through the one- or two-year hare decline. The first year of very low hare numbers was characterized by low adult survival (0.09-0.40), followed by higher survival in the one to two subsequent years of low hare densities (0.63-0.82) (Poole 1994; Slough and Mowat 1996,; O'Donoghue et al. 1997). A similar decline in the annual survival of bobcats was observed during a decline in jackrabbit density in Idaho (Knick 1990).

Survival tends to be lowest in winter. In southwestern NWT, cumulative survival summed over four years was higher during summer than during winter (0.91 vs. 0.08; Poole 1994). Most mortality during low hare abundance occurred during mid-December to mid-February, and most natural mortality (primarily starvation) appeared to coincide with <-35 °C temperatures, when metabolic requirements would be greatest (Poole 1994; O'Donoghue et al. 1995).

Causes of lynx mortality vary greatly across studies. Brand et al. (1976) noted that starvation of adult lynx seemed unlikely in all but the most pristine areas, suggesting that nutritionally stressed lynx are first predisposed to mortality related to humans. Ward and Krebs (1985) summarized studies to the mid-1980s of tagged lynx ($n = 36$) and found 95% of all lynx deaths were human related (mostly from fur-trapping), and only 5% of deaths were from natural causes. However, this result is probably biased by the fact that trappers provided their principal mode of recovery of dead animals. In interior Alaska, Stephenson (1986) estimated that annual mortality rates from trapping ranged from 55-100% of radio-marked lynx. On the Kenai Peninsula in Alaska, Bailey et al. (1986) suggested trapping was directly or indirectly involved in all nine lynx deaths on their study area during two years of high hare density, with trapping removing 80% of individuals over one year of age. On the same study area during a trapping closure, Staples (1995) observed that no adult male lynx died of natural causes during periods of low hare densities. Trapping mortality rates appear to be related to trapping pressure (generally driven by fur prices); seasonal trapping mortality in central Alberta increased two- to four-fold with a doubling of pelt prices (Brand and Keith 1979).

Earlier studies showed high trap-related mortality and essentially no natural mortality in lynx populations. On the basis of modeling population changes from combined harvest and field data, Brand and Keith (1979) concluded that trapping mortality of lynx tended to be additive. However, the authors' field samples were relatively small, and they could not distinguish between undetected mortality and dispersal (Hatler 1988). The recent Yukon (O'Donoghue et al. 1995, 1997; Slough and Mowat 1996) and NWT (Poole 1994) studies have documented significant natural mortality (primarily starvation) of lynx during the first two winters of hare scarcity (or second or third year of hare decline), which suggests that, at this period in the cycle, trapping mortality may be primarily compensatory to natural mortality at least in lightly or untrapped areas. The annual death rate from trapping (0.08) was higher than from natural causes (0.02) during peak and declining hare numbers in southwestern NWT (Poole 1994). However, during low hare numbers the death rate was far higher from natural causes (0.48) than trapping (0.20). In south-central Yukon, the annual survival rate on the study area was 0.40 in the first full year of low hare densities, with all detected mortality from natural causes (Slough and Mowat 1996). However, 20 marked lynx (27% of all emigrants) were trapped after dispersal, and 92% ($n$ = 25) of known emigrant deaths were human-caused, primarily by trappers (Slough and Mowat 1996). Comparing survival rates among studies can be problematic because rates can be affected by how researchers dealt with emigrants. Trapping returns alone will bias mortality rates, since little natural lynx mortality is detected (e.g., Ward and Krebs 1985).

Causes of natural mortality of lynx are difficult to determine; a radiocollar and tufts of hair provide little basis for inference. Ideally, mortality factors should also be identified as proximate or ultimate causes. Starvation (and related conditions) and cases of cannibalism of lynx have been recorded, primarily during periods of low prey abundance (Poole 1994; O'Donoghue et al. 1995; Slough and Mowat 1996). Predation on lynx by wolverine, wolf and coyote have also been confirmed (Slough and Mowat 1996; O'Donoghue et al. 1995; 1997; Chapter 4). Lynx host a diverse parasitic fauna, including nematodes, cestodes, trematodes, lice, and fleas (van Zyll de Jong 1966; McCord and Cardoza 1982; Smith et al. 1986; Quinn and Parker 1987), but parasite influence on lynx health and survival is unknown.

In summary, northern lynx populations subject to cyclic hare densities and differing trapping pressures exhibit large differences in mortality rates and causes. In lightly trapped or untrapped populations, population growth is characterized by high kit and adult survival that extends into the decline in hare numbers, followed by an increase in natural mortality (starvation, predation, and cannibalism) coupled with high dispersal (see next section) (Poole 1994; Slough and Mowat 1996; O'Donoghue et al. 1997). This pattern may be disrupted in areas with heavier and consistent trapping pressure, resulting in natality rates insufficient to maintain normal cyclic changes in populations through an entire cycle (Bailey et al. 1986).

## Movements and Dispersal

Daily movements of lynx within their range vary greatly and appear to be affected by environmental conditions, primarily prey densities and snow characteristics (Nellis and Keith 1968; Ward and Krebs 1985). Daily travel distances are generally calculated by three methods: (1) snow-tracking to determine cumulative distance moved over a 24-hour period (e.g., Brand et al. 1976; O'Donoghue et al. 1998b); (2) radiotelemetry to determine either straight-line distances between midday locations in successive days (e.g., Ward and Krebs 1985; Poole 1994); or (3) between paired fixes separated by 0.25-2 hours (Parker et al. 1983; Breitenmoser et al. 1991). Based on snow-tracking, average daily cruising distance ranges from 5-9 km (study means from Saunders 1963b; Nellis and Keith 1968; Parker 1981). Daily cruising distances provided by sequential (one to two hours) telemetry locations from a study on Cape Breton Island, Nova Scotia, were slightly greater in summer (about 9 km) than in winter (8 km; Parker et al. 1983). However, daily travel distances of lynx of 12.9-13.5 km in summer and 20.5 km in winter were measured during one year of the cyclic decline in the southwest Yukon (Breitenmoser et al. 1991). It may be assumed that females with young kittens have more restricted movements (Kesterson 1988; Mowat and Slough 1998).

The causes of changes to or differences in movement patterns of lynx are unclear. Studies in Alberta found increases in daily movements with increased hare density; Nellis and Keith (1968) speculated that the observed differences were due to differences in snow characteristics. However, Ward and Krebs (1985) documented a doubling of daily cruising radius (straight-line distance between successive 24-hour locations) from 2.7 to 5.4 km during moderate to high and low hare densities (<0.5 hares/ha), respectively, which they interpreted as increased foraging effort with decreased prey abundance. Similar conclusions can be drawn in southwestern NWT; daily travel distances as determined by radiotelemetry (24-hour locations) generally were greater ($p < 0.001$) after the decline in hare numbers (Poole 1994). Standardized track counts conducted daily on the same trails provide additional support; track counts tripled between years of similar lynx densities but from peak to declining hare densities (K. Poole, unpublished). However, studies in the southwest Yukon detected no significant changes in the percent time spent active by lynx during a cyclic decline (O'Donoghue et al. 1998b), highlighting the inconsistency of results among studies.

Most information on long-distance movements by lynx comes from animals caught by trappers. The number and locations of returns from trappers are affected by the density and distribution of trapping around study areas, and by behavioral differences in trap vulnerability among age and sex classes of lynx (Bailey et al. 1986; Quinn and Thompson 1987; Slough and Mowat 1996; Poole 1997). Therefore, all dispersal rates and distances reported must be considered potentially biased.

Long distance (>100 km) movements of lynx were once thought of as anomalies (Nellis and Wetmore 1969; Mech 1977), but are now considered characteristic (Ward and Krebs 1985; Brittell et al. 1989; Perham et al. 1993; O'Donoghue et al. 1995, 1997; Slough and Mowat 1996; Poole 1997). Documented straight-line dispersal distances range up to 1,100 km, with 15 documented cases of dispersal >500 km (Ward and Krebs 1985; Slough and Mowat 1996; O'Donoghue et al. 1997; Poole 1997; Fig. 9.3). Relatively intensive radiotelemetry efforts up to 200 km from the NWT study area center detected a uniform dispersal direction for female lynx, and a male dispersal favoring south and west (Poole 1997). Dispersing lynx crossed roads and large rivers and lakes, sometimes during the snow-free season. The minimum daily travel rate during dispersal averaged 4.6 km/day

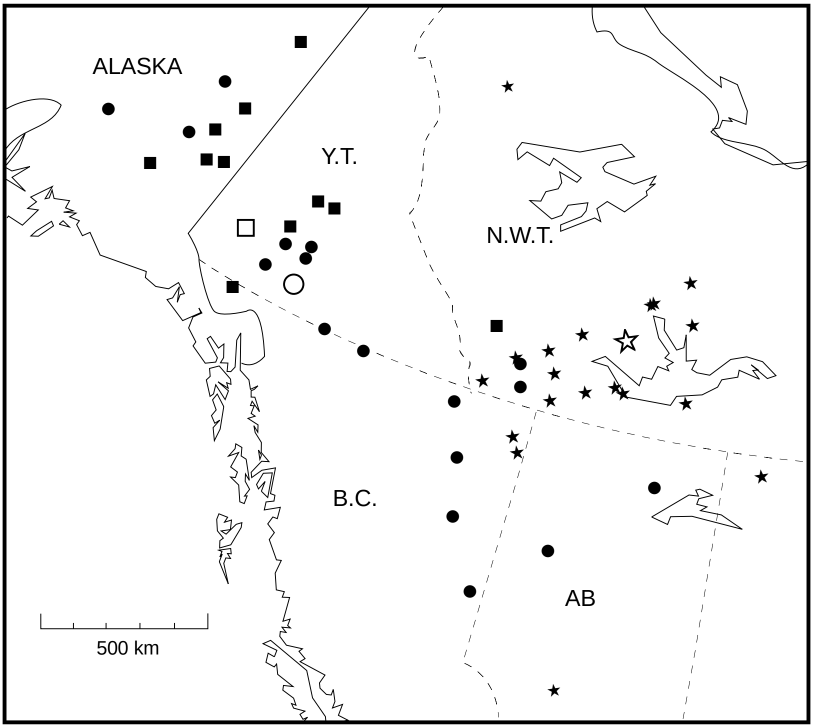

**Figure 9.3**—Dispersal of lynx >100 km from three areas in the NWT and Yukon. Data are taken from: ■ = Ward and Krebs (1985) (3) and O'Donoghue et al. (1997) (8); ● = Slough and Mowat (1996) (17); and ★ = Poole (1997) (19). Hollow symbols denote study area centers.

(range 1.7-8.3; *n* = 3; Ward and Krebs 1985), 4.2 km/day (0.3-23.6; *n* = 8; Slough and Mowat 1996), and 2.7 km/day (range 1.0-8.4, *n* = 10, Poole 1997) in three studies in the Yukon and NWT. These data suggest that dispersing lynx do not travel any farther per day than resident lynx.

Although emigration and immigration of lynx occurs throughout the hare cycle (Slough and Mowat 1996; O'Donoghue et al. 1997), a cyclic pattern is apparent. The rapid increase phase in lynx populations in south-central Yukon was at least partially due to immigration rates (21-38%) balancing or exceeding losses to emigration (0-33%; Slough and Mowat 1996). Emigration rates (52-79%) increased and exceeded immigration (12-50%) during the two-year decline in hare abundance and the first full year of low hare densities. In southwestern NWT, annual probability of dispersal for adult lynx was low (<24%) at peak hare densities and up to the spring after the hare crash (Poole 1997). Dispersal of adults primarily occurred in the spring after the rapid decline in hare abundance and during the first two winters of low hare numbers (78-100%; *n* = 9-16), and then stabilized during the third and fourth winters of low hare densities (<20%; *n* = 10) (Poole 1997). In southwestern Yukon, all three long-distance dispersals of resident adults occurred at the end of the snowshoe hare decline, with movements stabilizing during the subsequent winter (Ward and Krebs 1985). During a study of the same population a decade later, six of 15 collared lynx dispersed during the first year of a two-year snowshoe hare decline (O'Donoghue et al. 1995). Similar patterns of dispersal have been observed in bobcats (Hornocker and Bailey 1986; Knick 1990).

Annual timing of dispersal varies. Timing of dispersal may be related to the type of dispersal being observed. One type is juveniles dispersing from natal areas ("innate dispersal": a spontaneous movement related to the genetics of the dispersing individual). Another type is adults dispersing in response to an environmental "catastrophy" ("environmental dispersal": a behavioral response to unfavorable conditions; Howard 1960), such as the hare decline faced by northern lynx populations every 10 years. Juveniles would tend to disperse primarily in the spring, soon after independence. In lynx populations, we would expect most environmental dispersal to occur during the period of greatest nutritional stress, generally mid-winter. The period of greatest dispersal was March-June in south-central Yukon (Slough and Mowat 1996), and during mid-winter of the second year of the hare decline in southwestern Yukon (O'Donoghue et al. 1995). In southwestern NWT, most dispersal took place during March-June after the winter hare decline and during mid-winter of the subsequent two winters (Poole 1997).

Known immigrants to the south-central Yukon study area were more often adult males (Slough and Mowat 1996). During increasing, peak, and the initial decline in hare abundance, independent kittens 10-12 months of age and yearlings form the bulk of emigrants. Adults are most of dispersers during the latter portion of the decline and initial years of low hare densities (Slough and Mowat 1996; Poole 1997). Although male lynx have larger home ranges and hence increased mobility, male-biased dispersal rates in adult lynx have not been documented (Slough and Mowat 1996; Poole 1997). In addition, there were no differences in dispersal distances between sexes, or between kitten/yearling and adult age classes (Poole 1997). We do not feel we can conclude juvenile dispersal is even among the sexes due to lack of data.

Although emigration was apparently not sex-biased in the south-central Yukon study, 14 of 17 detected dispersals >100 km were by males (Slough and Mowat 1996). Most of these samples were from trapping returns, which are inherently biased toward males (Bailey et al. 1986; Quinn and Thompson 1987). Dispersal rates or distances are generally greater for males than females of most mammalian species (Greenwood 1980; Wolff 1994).

Annual survival rates did not differ for dispersing vs. non-dispersing lynx in southwestern NWT for any interval between the peak and the fourth year of low hare densities (Poole 1997). Survival of dispersing lynx was high (85-91%) during the peak and initial decline in hare abundance and the second to fourth years of low hare densities, and poor (29%) during the first full year of low hare densities (Poole 1997). Natural causes (largely starvation) accounted for over twice as many deaths of dispersing lynx than human-related causes (13 vs. six). Many lynx apparently died of natural causes en route, shortly after initiating dispersal, which suggests that the strategy used by lynx was to maintain residency until a critical starvation "stress point" was reached and then seek to disperse (O'Donoghue et al. 1995; Poole 1997). Initiation of dispersal often appeared to coincide with temperatures <-35 °C, a period when metabolic requirements would be greatest and prey diversity would be minimal, thereby increasing nutritional stress (O'Donoghue et al. 1995; Poole 1997). Given the regional extent of low snowshoe hare densities (Keith 1990; Poole and Graf 1996) many lynx never reached areas of higher prey density.

Some dispersing lynx survived the hare population low and re-established home ranges some distance from their point of dispersal (verified at 65-85 km, potentially up to 1,000 km; Slough and Mowat 1996, O'Donoghue et al. 1997; Poole 1997). These successful re-establishments of home ranges are difficult to detect using conventional study methods and are likely under-reported. Long-distance dispersal of lynx and other predators during cyclic declines could act as a synchronizing element of the hare cycle (Butler 1953; Lack 1954; Korpimäki and Krebs 1996; O'Donoghue et al. 1997).

Recent studies have documented the dispersal patterns of adult lynx during much of the cycle. More research is needed to examine dispersal of juveniles, which likely occurs throughout the cycle, but peaks when both hare and lynx numbers are increasing or high (Hatler 1988; Slough and Mowat 1996; Poole 1997). Further understanding of the factors affecting juvenile dispersal, such as the influence of sex and matrilineal relationships and prey density, will have implications for harvest management and the expansion and maintenance of more southern, non-cyclic lynx populations. Similarly, an understanding of the influence of habitat availability and connectivity (including forest fragmentation caused by timber harvest) on both juvenile and adult lynx dispersal will aid in management of southern populations.

## Harvest Management

Trapping mortality may be primarily compensatory to natural mortality during the first two years of lynx decline when natural mortality rates are high, but not during other periods of the cycle (Poole 1994; O'Donoghue et al. 1995, 1997; Slough and Mowat 1996). While the effects of harvest during the cyclic low could be severe, sustainable harvests can be high during the later cyclic increase and peak phases because growth rates are large (Poole 1994; Mowat et al. 1996b; Slough and Mowat 1996).

Lynx harvest records show a harvest cycle that varied dramatically in pattern over the past two centuries (Fig. 9.4). The harvest cycle can be

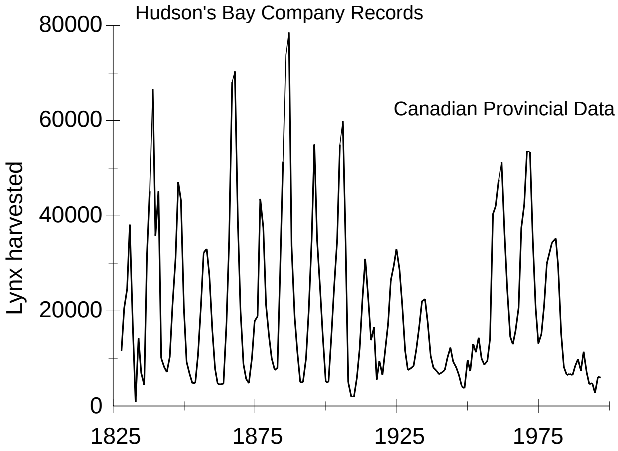

**Figure 9.4**—Lynx harvest in Canada from 1825 to 1997. Data prior to 1919 are from the Hudson's Bay Company and therefore do not represent the entire lynx harvest for Canada. After 1919, data were collected for each province and territory. (Data for 1827-1908; 1919-1983 from Novak et al. 1987. Data for 1910-1918 from Elton and Nicholson 1942. Data for 1984-1997, unpublished.)

characterized as having uniform high amplitude through to the early 1900s, declining amplitude from the 1920s to the 1950s, three fairly "normal" harvest cycles from the late 1950s to the early 1980s, and reduced amplitude during the 1990s peak. The cyclic pattern through the 20th century was relatively similar among jurisdictions, although the two northern territories had a slightly more distinct 1990 cyclic peak (Fig. 9.2).

Citing declining harvest returns and anecdotal information, De Vos and Matel (1952) noted a decrease in lynx numbers and distribution in Canada between 1920 and 1950. They cited overtrapping and ecological changes in habitat, primarily as a result of forest harvesting, as the main factors responsible for the decrease. We believe overtrapping may be the more probable explanation because forest harvesting as conducted in the early part of the century (high-grading) was unlikely to have caused a widespread decline in lynx numbers and distribution. Similarly, several authors have suggested local populations were overexploited during the cyclic low of the 1980s (Todd 1985; Bailey et al. 1986; Hatler 1988). There is little doubt that trapping can reduce lynx populations. Todd (1985) argued that recovery from low population levels may be prolonged, and that it took more than one hare cycle for lynx to recover from the suspected over-harvest during the 1920s and 1930s. However, harvest returns are affected by the host of factors influencing trapper effort and success, including changes in socioeconomic conditions, season length, quota and trap type restrictions, fur prices, subsidies, mode of transportation, and ease of access. Fur prices likely affect harvest effort over the short term (Brand and Keith 1979), but it may not be valid to compare and contrast inflation-adjusted prices and harvests that occurred decades apart. Harvest returns, therefore, may be roughly indicative of, but do not directly represent, real population changes.

There remains considerable debate whether lynx were significantly over-harvested during the 1980s and early 1990s (Todd 1985; Hatler 1988; Nowell and Jackson 1996). Interestingly, this period came after three cycles from 1960 to 1980 characterized by relatively high peak harvests, and, possibly more importantly, relatively high harvest levels during the cyclic lows (Fig. 9.4). Peak harvests (summing the five-year harvest around each peak) from 1960 to 1980 were similar to peak harvests during the classic cycles of the late 1800s, but the five-year harvest during the lows of 1960 to 1980 were about 25% higher than the lows of the late 1800s. Snowmobiles became readily available in the late 1950s and early 1960s, likely influencing trapper coverage, access, and attitudes. Whether or not these increased harvest levels during the cyclic lows had a significant cumulative impact on subsequent population levels is unknown. Harvest levels during the 1990 peak were significantly below earlier peaks observed during the 1960s and 1970s, which, in our opinion, is not unexpected given the 10-fold decrease in pelt prices over the last half of the 1980's, and hence lower trapper effort. This decrease in trapper effort was real; for example, NWT trappers told us that they were not interested in spending money on gas and equipment for a $60 lynx pelt when they received over $600 per pelt only a few years earlier. Many turned to wage jobs rather than trapping; the number of trappers in the NWT dropped from about 3,200 in the mid-1980s to 1,400 in the early 1990s (NWT Department of Renewable Resources, unpublished). Thus the decrease in harvest was at least partially due to decreased trapper effort in an area where lynx numbers appeared to be cycling normally (Poole 1994). In addition, based on community fur returns and local knowledge, no decrease in range has been detected in the two northern territories or Alaska through the 1990s (K. Poole, B. Slough, H. Golden, unpublished). Although we acknowledge that the amplitude of lynx abundance may have been decreased somewhat through the 1980s and 1990s, based on this coarse analysis we have no evidence to conclude that there was a long-term impact to contiguous northern lynx populations due to over-harvest during the low of the 1980s.

The long-term impact of high harvest pressure during the mid-1980s low phase in the lynx cycle on more southerly populations or where trapping intensity was severe may have been more significant (Todd 1985; Bailey et al. 1986; Hatler 1988). Ease of access in some areas (such as seismic lines spaced at one kilometer intervals blanketing parts of central and northern Alberta and British Columbia) coupled with extreme trapping pressure driven by high pelt prices during low lynx abundance may have reduced or eliminated lynx from some areas. In response to concerns about overharvest of lynx during the 1980s low, most Canadian provinces and Alaska implemented season reductions, reduced quotas, or harvest closures in at least portions of their jurisdictions in the late 1980s. The reduced harvest levels observed during the lynx cyclic peak of the early 1990s (Figs. 9.2, 9.4) were likely due to a combination of decreased trapper effort resulting from reduced pelt prices, and harvest restrictions that remained in place through much of the early 1990s; overharvest during the 1980 cyclic low may also have been a contributing factor. Given continuing low lynx pelt prices and trapper effort, we contend that in time, dispersal by lynx from adjacent healthy populations will likely repopulate many depopulated areas. However, the amplitude of the recovery to normal cyclic populations may be reduced for more than one cycle.

Although lynx populations in some areas have been over-harvested, we suggest that despite limited harvest management over the past half century, normal cycles have persisted throughout much of their northern range. This observation does not negate the need for more intensive harvest management in areas of high trapping pressure or marginal habitat, especially during the cyclic low. Harvest management options include implementation of a tracking harvest strategy (Caughley 1977; Brand and Keith 1979) where trapping is curtailed or eliminated for three to four years following the lynx decline; maintenance of permanent untrapped habitat or refugia (Slough and Mowat 1996); and season or quota restrictions (Parker et al. 1983; Todd 1985; Bailey et al. 1986; Poole 1994; Slough and Mowat 1996).

A tracking harvest strategy has management appeal because the only information required to implement the system is crude knowledge of the timing of the lynx decline. This information can be inferred from harvest records. However, measuring pelt length is relatively cheap and yields information on juvenile recruitment leading to greater certainty in the timing of cyclic events (Slough 1996). In healthy populations, we recommend managers consider curtailing harvest beginning two years after lynx populations begin to decline. In areas where distribution is more constrained or harvest more intense, managers may prefer to restrict harvest starting one year after lynx numbers begin to decline. Harvest should be restricted for three to four years or until there is evidence of significant juvenile recruitment and population increase; track counts may be a cost-effective monitoring method (Thompson et al. 1989).

A refugia management strategy has less utility where harvest pressure is fairly continuous throughout the landscape. Large movements and home ranges by lynx during low hare densities dictate that individual traplines are often not large enough to support even one lynx, and therefore management activities must be prescribed on a regional basis. Protecting a viable population in a refuge would require planning at the scale of thousands of square kilometers because lynx persist at such low densities during the low phase, and trapping effort on the edge of a refuge could remove lynx that reside tens of kilometers inside the refuge (Carbyn and Patriquin 1983). We suggest that attempting to conserve lynx by establishing permanently untrapped refugia is only advisable where very large reserves currently exist; even then lynx may be overharvested from substantial areas outside the reserve if harvest effort is intense. Further, establishing a network of reserves is politically difficult.

Season restrictions are necessary in all areas for the traditional reasons of avoiding harvest during breeding activities and timing harvest to the period when pelts are prime. Further, restricting trapping for lynx until December or even January may reduce the chance that orphaned juveniles die after their mother is trapped, providing greater sustainable harvests and less risk to the population (Bailey 1981; Parker et al. 1983; Mowat 1993).

This effort may be particularly important in low-density populations. In heavily harvested areas or where lynx are at low densities or discontinuous distributions, quotas may be the only means to adequately limit harvest. Because of the ease with which lynx are trapped, even very short seasons such as one month will not necessarily ensure appropriate harvest levels. Quotas give the managers the greatest control over harvest levels; however, setting reasonable quotas requires information about population size and habitat quality. Few managers have this kind of information for an entire management jurisdiction. For most managers in the northern part of the range of Canada lynx some sort of tracking harvest strategy will offer adequate protection to lynx populations at an achievable cost. However, the most effective management option will depend upon a host of factors specific to each region, including the spatial distribution of trapping effort, lynx density and cyclic dynamics, habitat quality and distribution, and socio-political factors.

## Acknowledgments

We thank the many researchers, technicians, government personnel, and harvesters who have helped advance our knowledge of lynx in the northern boreal forest over the past decade. The NWT Department of Renewable Resources, the Yukon Department of Renewable Resources, and the Natural Sciences and Engineering Research Council of Canada provided the bulk of funding for much of the recent research from the two northern territories summarized here. Research from Kluane, Yukon, was conducted as a part of the Kluane Boreal Forest Ecosystem Project headed by C. J. Krebs. We thank B. G. Slough for providing his data on lynx den site characteristics. Lastly, we thank L. Ruggiero for inviting us to write this paper.

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