14

Other Mammalian Predators

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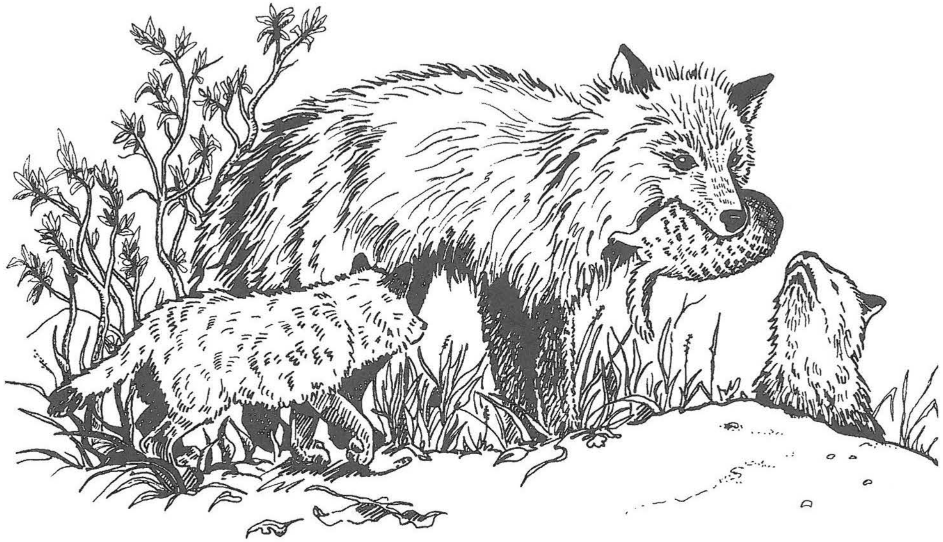

There were 12 species of carnivores that were confirmed living within the study area of the Kluane Project. We studied the population dynamics and behavior of only two of these, coyotes and lynx, because these were the two most closely associated with the snowshoe hare cycle. However, we also counted the tracks of all carnivores during winter and recorded direct observations year-round. In this chapter, we briefly summarize the information we gathered on other carnivores at Kluane and discuss interactions of the carnivore group as a whole with each other and their prey.

The cyclical changes in prey abundance that are characteristic of the Holarctic affect not only the main predators of the fluctuating prey, but also a wide variety of other predators that may track cycles and herbivores that are their alternative prey. In North America, both the 10-year cycle of snowshoe hares and the 4-year cycles of lemmings and some species of voles may cause cyclical dynamics in a wide variety of other mammals and birds (Finerty 1980, Keith and Cary 1991). In northern Fennoscandia, trends in numbers of voles are strongly cyclical with a 3- to 4-year period, and this cycle is also observed in abundance of their predators, grouse, hares, and shrews (Hörnfeldt 1978, Angelstam et al. 1985, Henttonen 1985, Lindström et al. 1994).

Boutin et al. (1995) documented changes in the populations of 22 species of vertebrates over 5–19 years at Kluane, including 5 carnivores. Here, we update and expand on their data and discussion.

14.1 Methods

We counted the tracks of all carnivores each winter (October through April) along a 25-km transect that traversed our study area, on days after fresh snowfalls while tracks were distinguishable. We calculated annual means and standard errors of these counts using means for the whole winter for each of eight segments of this transect (1.4–4.9 km in length, separated by topographical features), standardized to tracks per track night per 100 km. These counts gave us indices of the numbers of predators present each winter and also information on the locations of animals that we did not have radio collared (O'Donoghue et al. 1997). During winters when snowshoe hares were abundant (1987–1988 through 1991–1992), their tracks frequently obscured the tracks of other smaller animals, so we only counted the number of weasel tracks on the day after snowfalls for the analyses presented here. From 1986–1987 through 1996–1997, we counted tracks along 12,194 km of transect.

We also recorded the numbers and locations of all tracks of other carnivores that crossed the trails of coyotes and lynx while we were snow tracking (chapter 13). The locations of these trails changed among winters (O'Donoghue et al. 1998), so we used these counts to indicate use of habitats by other predators relative to those used by coyotes and lynx, rather than as indices of abundance among years.

14.2 Red Fox

Red fox, *Vulpes vulpes,* and their tracks were regularly but infrequently observed in the Kluane study area from 1986 through 1997. The number of tracks counted along our transect remained fairly low in all winters except 1991–1992 (figure 14.1). During that

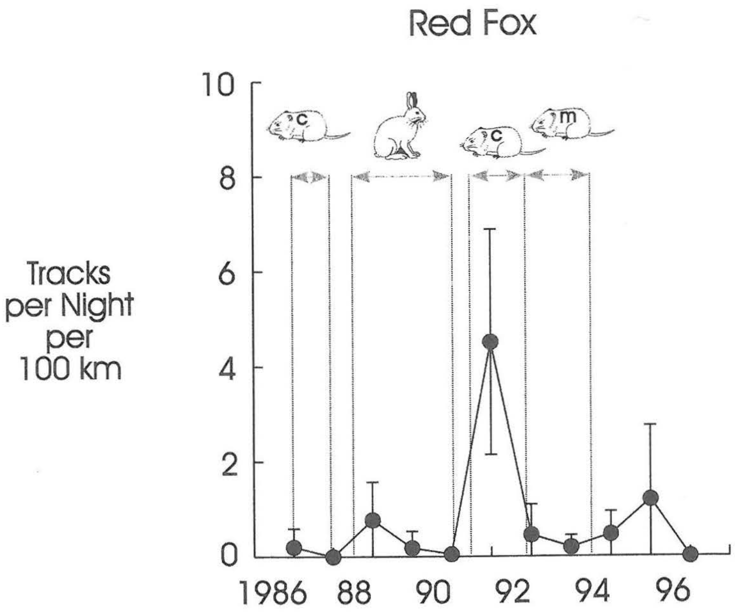

Figure 14.1 Abundance of tracks (± SE) of red foxes along a 25-km transect run with snowmobiles during winter from 1986–1987 through 1996–1997. Dashed lines demarcate periods of peak densities of *Clethrionomys* (>500 voles/100 ha; vole silhouettes marked with "c"), snowshoe hares (>125 hares/100 ha), and *Microtus* (>1000 voles/100 ha; vole silhouette marked with "m"). Captures of *Microtus* on forested grids indicate that they may have also reached high numbers in 1988, but their preferred meadow habitats were not trapped in that year.

winter, we observed a large influx of fox tracks in March on our transect (36 tracks in March, relative to an average of 6.3 fox tracks per whole winter in other years). Fox tracks were concentrated (87% of all fox tracks) in the first 9 km of the transect, mostly in two large, shrubby, open areas, in all winters except 1991–1992. During March of 1992, however, fox tracks were found along the entire transect, and only 39% of tracks were in this first section.

Based on incidental observations of their tracks, foxes were abundant in the alpine areas surrounding the forested part of our study area. In the valley, coyotes were much more abundant: we saw 10 times as many coyotes as foxes while in the field, and their tracks were 20 times more abundant. We suspected that only 1 radio-collared hare was killed by a fox in our study area, relative to 217 confirmed coyote kills. When hunting in the valley, foxes used habitats with less dense overstories than either coyotes or lynx (91% of their crossings of coyote and lynx trails were in habitats with less than 50% cover, relative to 60% use of these habitats by coyotes and lynx; $n = 32$, $\chi^2 = 8.33$, $p = 0.004$). While live trapping for coyotes and lynx, we trapped four red foxes—one a juvenile male, and three adult males. The mean weight of the adults was 6.5 ± 0.9 (SD) kg.

In summary, we saw little evidence that red foxes responded numerically to either changes in the numbers of hares or voles in our study area. However, as foxes were likely more abundant in alpine areas surrounding our study area, we may have missed any changes in fox numbers that did occur. The large increase in the number of fox tracks that we observed in 1991–1992 may have been the result of increased movements of foxes, resulting from the cyclic decline in numbers of hares or ptarmigan at higher elevations. We did not measure the numbers of hares in the zones of dense subalpine willows, but they were abundant there at the peak in hare abundance. In a study area approximately 60 km from ours, foxes hunted hares heavily in areas of dense shrubs at a cyclic peak and early decline (Theberge and Wedeles 1989), but relied more heavily on alternative prey, mostly voles and ground squirrels, when hares were less abundant (Jones and Theberge 1983).

Our results contrast with the conclusions from fur records that suggest populations of red foxes may show 4-year or 10-year cycles in North America, depending on their main prey (Finerty 1980). Likewise, in northern and central Fennoscandia, numbers of foxes fluctuate in 3- to 4-year cycles with those of voles (Hörnfeldt 1978, Angelstam et al. 1985, Lindström 1989), and both observational and experimental data suggest that the resulting cyclical predation by foxes may contribute to cycles in numbers of grouse and hares, alternative prey of the foxes (Marcström et al. 1988, 1989, Small et al. 1993, Lindström et al. 1994).

In our study area, foxes may have avoided using the valley because of the presence of coyotes. There is ample evidence from elsewhere in their range that the presence of coyotes generally leads to lower numbers of foxes (Peterson 1995), and this is supported by local accounts of much higher fox numbers in our study area before coyotes colonized the region. Foxes are sometimes directly killed by coyotes (Peterson 1995), and they frequently establish their home ranges (Major and Sherburne 1987, Harrison et al. 1989) and dens (Voigt and Earle 1983, Sargeant et al. 1987) outside or on the periphery of coyote territories.

On a worldwide basis, red foxes are most abundant in areas with heterogeneous habitats and, unlike coyotes, their range extends into the tundra (Larivière and Pasitschniak-Arts 1996). Foxes regularly use open habitats, especially when snow depths are lower and voles are more vulnerable to predation (Halpin and Bissonette 1988, Lindström and Hörnfeldt 1994). Local differences in habitat use may allow coyotes and red foxes to persist where they are sympatric (Major and Sherburne 1987, Theberge and Wedeles 1989). The subalpine shrubby areas around our study area were seldom used by coyotes or lynx until late in the cyclic decline of hares. When lynx moved into these areas in 1992–1993, we observed one case of predation by lynx on a fox (O'Donoghue et al. 1995). In Alaska, there are a number of records of lynx preying on red foxes, especially during cyclic lows of hares (Stephenson et al. 1991). Changes in predation pressure on foxes may therefore be an indirect effect of the hare cycle on their abundance.

14.3 Wolf

Wolves, *Canis lupus,* were present each year in our study area, and the abundance of their tracks fluctuated irregularly along the track transect during this study (figure 14.2). One pack of wolves passed through the area periodically, and signs of single animals were seen more frequently; group sizes ranged from one to nine. We observed the most wolf tracks during the winter of 1989–1990, at the peak of the hare cycle (figure 14.2), but

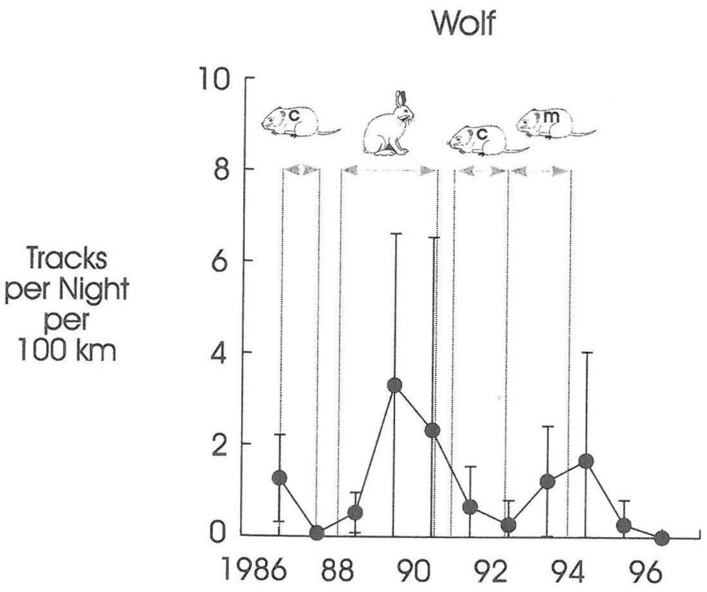

Figure 14.2 Abundance of tracks (± SE) of wolves along a 25-km transect run with snowmobiles during winter from 1986–1987 through 1996–1997. Dashed lines demarcate periods of peak densities of *Clethrionomys* (>500 voles/100 ha; vole silhouettes marked with "c"), snowshoe hares (>125 hares/100 ha), and *Microtus* (>1000 voles/100 ha; vole silhouette marked with "m").

numbers were highly variable. The percentage of observations that were of lone wolves changed from 40% during the cyclical increase (6 of 15 observations), to 84% at the peak (16 of 19), to 57% during the decline (4 of 7), to 20% at the low (1 of 5).

There is no clear evidence of a 10-year cycle in numbers of wolves in North America (Finerty 1980). Although wolves regularly prey on snowshoe hares, ungulates are their main prey throughout their range in North America (Mech 1970, 1974, Banfield 1974). Hares may represent 1–2% of their diet in winter (Carbyn et al. 1993), and up to 12% in summer (Thurber et al. 1992, Carbyn et al. 1993). In our study area, only four radio-collared hares were killed by wolves.

Our data suggest that the percentage of lone wolves was highest when the abundance of hares was at its peak. Wolves have been observed actively hunting hares, and a superabundant supply of hares could increase the survival of lone animals. However, despite many studies of wolves, there are no clear data that indicate a direct link between the hare cycle and wolf survival. The abundance of moose was low (<0.1/km^2), and there were no caribou in our study area, which may increase the frequency of solitary living by wolves (Messier 1985). Our data on numbers and group sizes of wolves were likely affected in later years by a wolf-control program started by the territorial government in 1993 north of our study area.

Wolves may exclude coyotes over large areas (Peterson 1995), and, locally, coyotes avoid areas frequented by wolves in some places (Thurber et al. 1992). Exclusion of coyotes benefits red foxes, so if densities of wolves in our study area had been higher, red foxes may have been more abundant in the valley, as proposed by Peterson (1995).

14.4 Weasel

There were two species of weasels present in our study area, the short-tailed weasel or ermine, *Mustela erminea,* and the least weasel, *Mustela nivalis.* We did not distinguish between their tracks, but based on our observations, short-tailed weasels were more abundant. Numbers of weasels remained low from 1986–1987 through 1990–1991, based on our track transect, and then increased steadily to a high in 1994–1995 (figure 14.3). The period of increase corresponded with successive highs in the abundance of red-backed voles and *Microtus,* with peak numbers of weasels occurring in the winter after the decline in *Microtus* abundance (see chapter 10). The number of weasel tracks declined again by the winter of 1995–1996.

Weasels were mostly found in more open habitats along the trails of coyotes and lynx. Approximately 39% of their crossings were in habitats with less than 25% overstory cover, relative to 22% of this habitat available (χ^2 = 154.16, $p < .0001$). This was especially

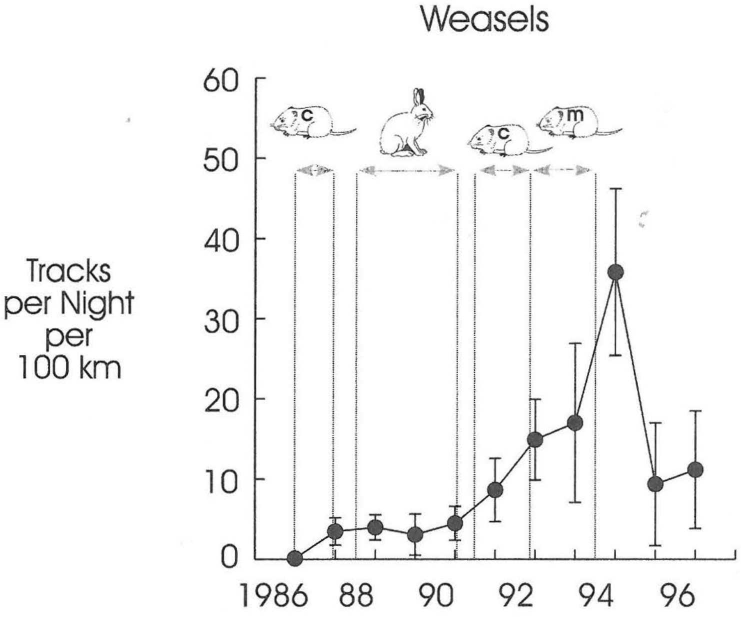

Figure 14.3 Abundance of tracks (± SE) of short-tailed and least weasels along a 25-km transect run with snowmobiles during winter from 1986–1987 through 1996–1997. Dashed lines demarcate periods of peak densities of *Clethrionomys* (>500 voles/100 ha; vole silhouettes marked with "c"), snowshoe hares (>125 hares/100 ha), and *Microtus* (>1000 voles/100 ha; vole silhouette marked with "m").

true in years when *Microtus* were abundant; before 1992–1993, weasels used these open habitats as expected.

Our data show that weasels did not respond numerically to the snowshoe hare cycle in our study area. This is contrary to evidence from incidental trapping in studies in Alberta (Keith and Cary 1991), where weasels (*M. erminea* and *M. frenata*) did show a 10-year cycle in numbers. Based on fur records, however, there is no evidence that the hare cycle affected the abundance of short-tailed weasels (Finerty 1980). Weasels killed only two radio-collared hares in our study area.

Weasels clearly responded to the 1991–1994 increase in numbers of voles at Kluane, and their population trend was correlated with that of *Microtus* in meadow habitats during our study with a 1-year lag ($r = .87$, $p = .027$). Voles are the main prey of weasels throughout their circumboreal ranges (King 1983, Sheffield and King 1994). There is ample evidence that weasels show strong numerical responses to changes in vole abundance in many areas (Fitzgerald 1977, Tapper 1979, Korpimäki et al. 1991). Short-tailed weasels have delayed implantation (King 1983), and hence their numerical responses to changes in prey abundance are typically delayed. Empirical studies in northern Fennoscandia show that the abundance of weasels (*Mustela nivalis*) fluctuates cyclically, following the 3- to 4-year cycles in numbers of voles, mostly *Microtus agrestis* (Korpimäki et al. 1991, Korpimäki 1993). These data have been used in models to suggest that predation by the specialist weasels causes the cyclic dynamics of voles in northern Fennoscandia (Hanski et al. 1991, 1993, Hanski and Korpimäki 1995).

Our index of weasel abundance was not correlated with density estimates of *Clethrionomys* (chapter 10). Although 3- to 4-year cycles are characteristic of some populations of voles in North America (Krebs and Myers 1974), abundance of *Clethrionomys* generally does not cycle regularly (Gilbert and Krebs 1991). In our study area, numbers of red-backed voles were high in 1984, 1987, and 1991–1992 (Gilbert and Krebs 1991, Boutin et al. 1995). We did not see a numerical response of weasels to high numbers of red-backed voles in 1987. Although the abundance of *Microtus* was not monitored in meadow habitats before 1989, captures on forested grids suggest that they reached high numbers in 1988 (chapter 10). The peak in numbers of voles in 1987 and 1988 was of shorter duration and, at least for *Clethrionomys,* of lower densities than the peak in the 1990s; this may be why weasels did not respond to the 1987–1988 vole peak.

We suggest that the abundance of weasels in our study area was limited by low densities of small mammals, particularly in spring. Erlinge (1974) and Tapper (1979) found that least weasels required minimum spring densities of field voles (*Microtus agrestis*) of 10/ha and 14/ha in southern Sweden and England, respectively, before they would breed. The densities of voles at Kluane seldom approached those levels (chapter 10). In addition, only about 7% of our study area consisted of the meadow habitats preferred by *Microtus,* which are apparently more susceptible to predation than *Clethrionomys* (Henttonen et al. 1987).

The use of more open habitats by weasels at Kluane likely reflects their preference for hunting *Microtus.* Throughout their range, weasels use a wide range of habitat types, but generally avoid dense forest and open areas with no shelter (King 1983, Sheffield and King 1994). Risk of predation is thought to cause the avoidance of open areas, but during winter, weasels have subnivean refuges from many predators, and they can hunt in meadows with more protection.

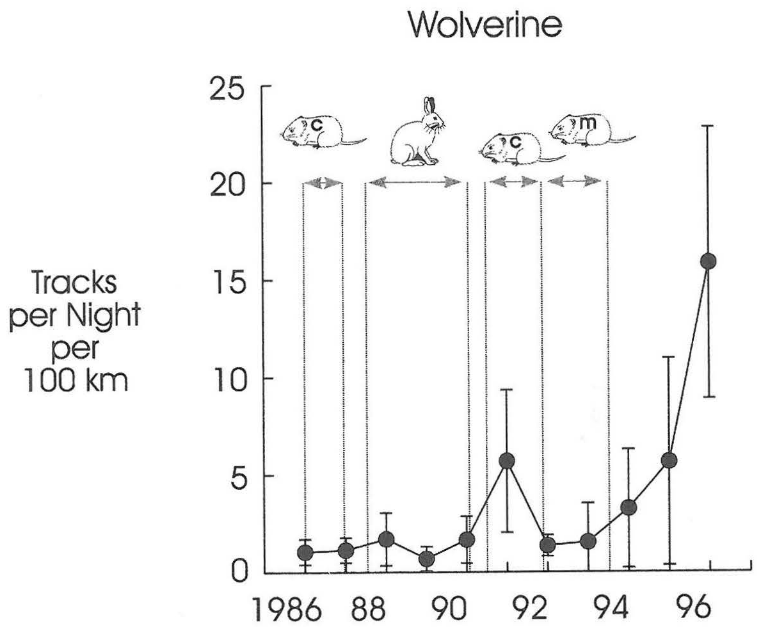

Figure 14.4 Abundance of tracks (± SE) of wolverines along a 25-km transect run with snowmobiles during winter from 1986–1987 through 1996–1997. Dashed lines demarcate periods of peak densities of *Clethrionomys* (>500 voles/100 ha; vole silhouettes marked with "c"), snowshoe hares (>125 hares/100 ha), and *Microtus* (>1000 voles/100 ha; vole silhouette marked with "m").

14.5 Wolverine

Wolverines, *Gulo gulo,* were regular residents in the Kluane study area. They typically travel over large home ranges in the north (up to over 900 km^2; Banci 1994), so it is likely that the home ranges of wolverines using our study area also extended into the alpine areas around it. The abundance of wolverine tracks along our track transect stayed fairly constant and low in all winters but 1991–1992 until 1994–1995, when numbers of tracks began to increase until the last winter of our study, 1996–1997 (figure 14.4).

Our data show no clear evidence that numbers of wolverines were related to the abundance of hares or voles in our study area. Population trends from fur returns show some evidence of a 10-year cycle in North America (Finerty 1980). We do not know the cause of the increase in numbers of wolverine tracks during the last 3 years of this study, but our subsequent observations in the study area in 1997–1998 and 1998–1999 suggest that this increasing trend did not continue.

Throughout their range, wolverines are opportunistic feeders, and they eat a wide variety of prey, hares and voles included, and carrion (Pasitschniak-Arts and Larivière 1995, Banci 1994). Wolverines killed only two radio-collared hares in our study area, but studies in the Yukon have shown that hares are an important component of wolverine diets at both high and low phases of the hare cycle (Banci 1994).

14.6 Marten

Martens, *Martes americana,* were uncommon in our study area, despite the fact that most of the forest was mature spruce, their preferred habitat (Clark et al. 1987, Buskirk and Ruggiero 1994). Only three observations of martens were made during this study, and their tracks were recorded regularly but infrequently along the trails of coyotes and lynx. Martens are uncommon throughout a large area of the southwest Yukon (Slough 1989).

Voles, particularly *Microtus* when they are available, and *Clethrionomys* when they are not, are the staple food of martens throughout their range, but they also feed on a wide range of prey up to the size of hares (Clark et al. 1987, Buskirk and Ruggiero 1994). Martens killed only two radio-collared hares in our study area. Based on fur records, martens may show 4-year or 10-year cycles in abundance, depending on their main prey (Finerty 1980). We suggest that the abundance of martens in our study area, as with weasels, was limited by the low densities of small mammals.

14.7 Mink and Otter

Mink, *Mustela vison,* and river otters, *Lutra canadensis,* were both present along creeks and lakes in the Kluane study area. We seldom counted their tracks or made direct observations of either species, because of their restricted distribution.

Both species prefer streams and lakes with banks where they can use burrows created by beavers, or they use the lodges of beavers (Banfield 1974, Larivière and Walton 1998). In Alberta, incidental trapping records of mink suggested that their numbers cycle with a 10-year periodicity (Keith and Cary 1991).

14.8 Synthesis and Conclusions

Our data on the abundance of carnivores besides coyotes and lynx, although limited, suggest that their population trends were not tightly tied to those of hares at Kluane. Tracks of red foxes, wolves, weasels, and wolverines were encountered frequently enough in our study area that we would have detected large changes in abundance. Martens were uncommon, and mink and otters were restricted to riparian habitat, so our conclusions regarding these species are less robust.

Numbers of weasels were related to the abundance of voles, especially *Microtus.* Weasels did not respond numerically to high numbers of voles in 1987 and 1988, whereas they did increase from 1992 to 1995, when first *Clethrionomys* and then *Microtus* reached high numbers. Therefore, vole populations may need to be high for a number of years in order for numbers of weasels to increase in our study area. Population trends of other carnivores, notably red foxes, were not related to vole abundance in the Kluane study area.

The responses of boreal predators to cyclic fluctuations in numbers of their prey differ between North America and Fennoscandia. In central and northern Fennoscandia, 3- to 4-year population cycles of voles and their predators are the dominant influence in generating synchronous cycles for a host of alternative prey, including hares, grouse, and shrews. In the North American boreal forest, though, the 10-year cycle of snowshoe hares appears to be the main dynamic driving the population trends of larger vertebrate predators only, and these cycles may then be imposed on some alternative prey such as grouse and ground squirrels, but not on others such as voles and red squirrels. Boutin et al. (1995) speculated that the differences between the vertebrate communities in North America and Fennoscandia may be because of the numerical dominance of hares and the resulting evolution of larger-bodied predators that are inefficient at hunting voles, and the greater abundance of *Clethrionomys* than the more vulnerable *Microtus.*

There are no clear data showing that the abundance of wolves and their main prey, moose and caribou, are related to the hare cycle anywhere they coexist. The communities of large and small mammals may therefore function independently in the boreal forest. We did, however, observe changes in the frequency of lone wolves over the hare cycle at Kluane, and this relationship bears further study.

Relations among predatory species in the North American boreal forest are characterized by behavioral avoidance and intraguild predation (Polis et al. 1989) among many species (O'Donoghue et al. 1995). Sympatric carnivores typically use different habitats or prey species, which may reduce competition for resources (Rosenzweig 1966), as was the case for red foxes and coyotes in our study area. We do not know whether the predation that we observed among predators affected their abundance, or was mostly compensatory.

There is still a great deal to learn about how boreal carnivores are affected by cyclical fluctuations of hares and voles and how they interact with each other. Few studies have been devoted to examining the community relationships of the less abundant carnivores in boreal North America, and none, to our knowledge, has looked in detail at community structure and functional relationships among the whole group of carnivores. Long-term studies such as the Kluane Project and Keith's work in Alberta (Keith and Cary 1991) have gathered data indexing population trends of these species, but research specifically aimed at them will be necessary to further clarify their roles in the boreal food web.

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