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Predation and Animal Populations: Lessons from Lemmings and Geese

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WHAT DETERMINES THE SIZE OF A POPULATION OF ANIMALS? Does the population stop growing when food becomes scarce, or because predators or diseases kill an increasing proportion of individuals? Or do behavioural changes slow population growth? Many species, both in the North and elsewhere, are in decline or at risk. Unfortunately, we rarely know enough about the dynamics of their populations to be able to prescribe sure solutions. A better understanding of population processes would help wildlife biologists answer questions about threatened northern populations: Would the shooting of seals help the northern cod to recover? Are migratory songbirds declining because of habitat loss in the South? Why have Peary caribou dwindled in numbers throughout most of the Canadian Arctic Islands?

Wildlife scientists sometimes use "adaptive management" to assess the effectiveness of an intervention in altering population growth. Experimental populations, which receive a management "treatment," are compared to undisturbed control populations. For example, if predation were believed to be threatening wildlife, animals that prey on the experimental population might be culled.

Well-designed experiments with large animals like caribou or wolves are valuable but costly, and could themselves have unexpected detrimental consequences for the population. Instead, experiments can be performed with small, abundant animals as "models." Models are useful if, as scientists hope, general principles of population dynamics apply to populations with similar characteristics. Laboratory populations of captive organisms make the simplest models, but can mimic natural systems only to a limited degree. Arctic ecosystems are simple in the sense that they contain few species compared to temperate or tropical systems. Another compelling reason for studying arctic ecology is that we still know relatively little about it, and we need that knowledge to better protect and manage northern habitats and wildlife. The most abundant resident small vertebrate in the Arctic is the lemming, a rodent related to the mouse, but larger and with shorter legs and tail. Populations of lemmings grow and shrink cyclically, peaking every three to five years throughout most of the Arctic. Therefore changes in population size can be observed without manipulating the number of animals. These

Deb Wilson holds a collared lemming that has just received a radio transmitter.

characteristics make the lemming a good model for studying population dynamics.

Like the lemming, several other species of animals have cyclic population dynamics. A well-known example is the snowshoe hare. Widespread in the boreal forests of North America, hares peak in numbers about every decade. Researchers have successfully deciphered some of the underlying mechanisms. The mathematical explanation of

An arctic fox beginning to moult into its brown summer coat.

cycles is that a factor such as mortality or reproduction changes as population size does, but with a delay. Such a lag in part explains the snowshoe hare cycle (Krebs, 1996). As hares grow in numbers, predators like lynx and coyotes reproduce at an increased rate. The rise in predator numbers is delayed, however, because the predators' reproductive cycles are longer than that of hares.

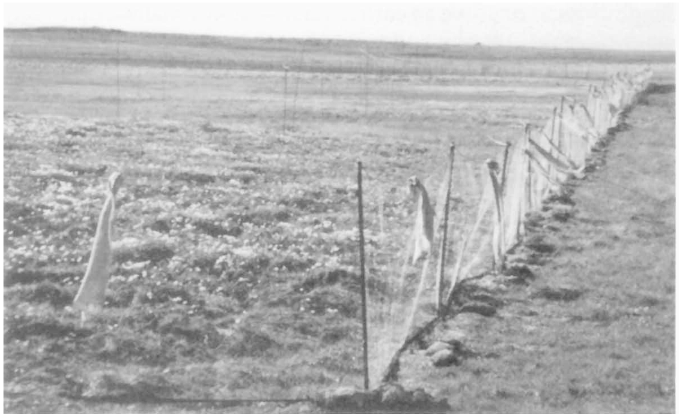
Predation is an important factor for lemming populations, too. The tundra is a dramatically different place during a lemming peak. Arctic foxes that might not otherwise breed rear large litters. Snowy owls, rough-legged hawks, and pomarine jaegers settle and nest in regions where lemmings are temporarily abundant. When researchers have placed radio transmitters on lemmings to determine causes of mortality, the majority of deaths have been due to predation. However, if predation were prevented, other sources of mortality, such as age, disease, or starvation, might become more important. Additionally, the reproductive rate of the lemmings may be low when their population density is high. Therefore, the lemming decline might occur even in the absence of predation.

Great swings in the number and behaviour of predators affect prey other than lemmings. If, when lemmings are plentiful, each arctic fox takes fewer birds or ground squirrels, the predation rate on these alternative prey might drop. On the other hand, because fox numbers increase through breeding during the lemming peak, the losses of alternative prey might rise. This second effect occurs in a delayed fashion in Scandinavia, where the predation rate on ptarmigan nests increases following vole peaks. With brent geese, which breed on the Taymyr Peninsula in Russia, both patterns are thought to occur (Summers, 1986). The proportion of juvenile brent geese in flocks returning to their wintering grounds in England is usually high after peak lemming summers, and low the following year. But in Dr. Robert Bromley's 11-year study of white-fronted geese (*Anser albifrons*) and Canada geese (*Branta canadensis*) on the Kent Peninsula in the Northwest Territories, fluctuations in nesting success were not completely synchronized with the lemming cycle.

Two questions emerge from this story that are of particular interest to me, and I designed my doctoral research to answer them. First, do predators cause the lemming decline? And second, how does the lemming cycle affect predation on goose nests? My research advisors are Dr. Anthony Sinclair and Dr. Charles Krebs at the University of British Columbia. I am collaborating with Bob Bromley on the second topic, and have done all my field research on the Kent Peninsula at his Walker Bay field station, which is managed by the Northwest Territories Department of Resources, Wildlife, and Economic Development. Walker Bay has two species of lemming, the collared lemming (*Dicrostonyx groenlandicus*) and the brown lemming (*Lemmus trimucronatus*). Both species cycle in numbers over a period of three years; I studied them in the summers of 1994 through 1997. Many species of predators eat lemmings, but at Walker Bay only three are important predators on both lemmings and goose nests: arctic foxes (*Alopex lagopus*), parasitic jaegers (*Stercorarius parasiticus*), and glaucous gulls (*Larus hyperboreus*).

I experimentally protected an 11-hectare patch of tundra from predators, with a fence to deter large predatory mammals and monofilament fishing line overhead to deter predatory birds. The population dynamics of lemmings within this exclosure can be compared to those of control populations outside. I counted and observed nest predators to determine whether their foraging behaviour changed in relation to the lemming cycle. I also did experiments with artificial plaster goose eggs to estimate changes in predators' interest in eggs. More details of my research methods are described in Wilson (1996). The results discussed below are preliminary, until I have completed proper statistical analyses.

My helpers and I completed the predator exclosure late in the summer of 1995. Lemming numbers peaked in the summer of 1996. By late July, the density of lemmings within the exclosure was higher than that outside. They seemed to cease reproducing in late summer, so some winter population decline was expected. In September I returned to Vancouver for the winter. By the spring of 1997, the lemming population had declined, and the density inside the exclosure was no longer significantly higher



The predator exclosure at Walker Bay, Kent Peninsula, Northwest Territories.

A juvenile collared lemming.

than that in control sites. The decline continued through the summer, but less markedly within the exclosure.

I cannot with certainty identify the cause of the winter decline. Some predators had learned to enter the exclosure—not surprising, given the abundance of lemmings inside. There may have been heavy autumn predation, as large numbers of young foxes and snowy owls were observed in the region before deep snow had accumulated. At present I am analyzing scats left by foxes and pellets left by owls, to estimate how many lemmings these predators could have killed. Predation by weasels appears to have been minor: we saw few weasels until well into the summer of 1997, and we found only two lemming winter nests with signs of occupation by weasels. Factors related to competition for food and space may have contributed to this early stage of the decline.

My knowledge of the summer decline is more complete. By putting radio transmitters on adult lemmings, we learned that weasels, foxes, and birds killed many in the control areas. We caught baby lemmings in the exclosure but almost none outside. It is likely that most juveniles born in the control sites were killed in the nest or soon after weaning.

Foxes were most abundant during the peak lemming year, with no lagged effect of increased abundance in the following year. Evidently, many of the foxes born during the peak year either died or emigrated that winter. Numbers of glaucous gulls were highest in the year before the peak. This surprising result was likely due to the spatial structure of the habitat. The gulls nest on islands in large lakes. In the peak and decline years they could feed on lemmings near their nests, and so had no need to forage throughout the study area. During the lemming peak compared to other years, I observed all three types of nest predator less often in the prime goose nesting area than in the study area as a whole. The few foxes that I saw in the goose nesting area during the peak spent less time in foraging activities than they did in other years; instead, I observed them resting and carrying their young between dens.

If these patterns occur in all three-year lemming cycles at Walker Bay, they yield the prediction that the number of goose nests lost to predators should be lowest during peak lemming years. They do not predict a particularly high predation rate during the year after the peak, because there was no one-year lag in the increased abundance of predators. Both Bob Bromley's estimates of nest predation and the attack rates on my artificial plaster eggs fitted this template in 1995 through 1997. However, patterns of nest loss vary among the earlier lemming cycles for which we have data. Variation in the time of year when lemmings increase and decline affects the winter survival of foxes, the spring abundance of predatory birds, and the diets of all the predators. In addition, the suite of predators in the region is not constant. In 1996, many pomarine jaegers bred at Walker Bay—an uncommon occurrence even during lemming peaks. These birds defended their nests aggressively against other predators, and in this way provided protection to the geese. It seems that in this ecosystem lemming abundance does affect the nesting success of geese, but not in a very predictable way.

I am encouraged by the results of the predator exclosure experiment, since reducing predation had clear effects on the lemming population in spite of the limitations of the structure. I am anxious for this experiment to be continued at Walker Bay or repeated elsewhere, with improved and replicated exclosures. In some years it will be desirable to continue experiments into the fall and winter, a difficult problem for professors and students with classes to teach or attend. An expanded experiment of this nature will be expensive but has a real chance of yielding new and unambiguous results.

The second part of my study emphasizes that a decline in abundance of one type of prey may have unexpected deleterious effects not only on its predators but also on other prey species. These observations may be relevant when outbreaks of disease kill prey animals, or when wildlife managers attempt to remove introduced pest species. To be able to make predictions about the population dynamics of alternative prey, it is necessary to take into account spatial patterns, delayed effects, the foraging behaviour of predators, and interactions among different species of predators.

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