Raison, J. K., and J. M. Lyons. 1971. Hibernation: alternation of mitochondrial membranes as a requisite for metabolism at low temperature. Proc. Nat. Acad. Sci. 68:2092–2094.

Richardson, T., and A. L. Tappel. 1962. Swelling of fish mitochondria. J. Cell. Biol. 13: 43–53.

Swan, H. 1974. Thermoregulation and bioenergetics. American Elsevier, New York.

HENRY SWAN
CHRISTOPHER SCHÄTTE

DEPARTMENTS OF CLINICAL SCIENCES AND PHYSIOLOGY AND BIOPHYSICS
COLORADO STATE UNIVERSITY
FORT COLLINS, COLORADO 80521
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HARES, LYNX, AND TRAPPERS

There have been recurrent controversies in the literature over different aspects of the population "cycles" of some species of northern animals. The arguments have ranged from whether the cycles are real or actually generated by chance (Cole 1951) to the nature of the causal relations between the population changes of herbivores, such as the snowshoe hare, and those of predators, such as the lynx. Many of the data fueling these debates have come from a remarkable set of statistics, namely, the Hudson Bay Company's record of furs bought from trappers during a period of about 220 yr. What has been almost entirely overlooked in these debates is that the trappers are predators in their own right and their fur harvests may not relate directly to the population numbers of the species they are trapping.

A number of investigators have shown statistically (Butler 1953; Keith 1963) and mathematically (Leigh 1968) that some of the fur cycles are not randomly generated and that the fluctuations are periodic. Hudson Bay Company records of lynx pelts, for example, show dramatic cyclical oscillations. Leigh examined one set of lynx records and mathematically calculated a cycle with a period of 8 yr.

In some cases peak harvests of lynx have been shown to follow just after peak populations of snowshoe hares, and the harvests of lynx declined after the hare population crashed. This led to early suggestions that the hare-lynx interaction exhibited a classical predator-prey relationship. According to this interpretation, the lynx increased in response to large numbers of available prey and the hare population declined due to the increased lynx predation, which in turn led to a crash in the lynx population. Keith (1963), however, pointed out that the hare population on certain islands oscillates in the absence of lynx. This suggests that the fluctuations in the hare population are due to factors other than increased predation.

The other side of this interaction, that of the possible increase of the lynx population as a response to an increase in the hare, has also come under fire.

There is no doubt that the harvest of lynx oscillated and that this oscillation was related to the hare population cycle. The question is whether the increase in pelts was a proportional reflection of an increase in the lynx population which resulted in turn from an increased food supply. The rapidity with which the lynx pelt sales increased during the population increase in hares is itself suspicious. Although lynx may breed at 1 yr of age (Palmer 1957), they only have a single litter of young a year, with an average of two to three kittens (Banfield 1974). Even under optimum food conditions we would expect the kinds of dramatic increases that are seen in the Hudson Bay Company's fur records to take a number of years. Instead, Leigh found that the numbers of lynx were most closely correlated with the abundance of hare of the previous year. According to his calculations there should have been a time lag of 4–6 yr.

Gilpin (1973) took the same data used by Leigh and subjected it to "graphical predation theory" analysis. Through this exercise he generated a graphical configuration which suggested that the hare was the predator of the lynx or, looking at it more realistically, that an increase of hare indirectly kills lynx. He postulated two possible indirect effects which an increased hare population might have on lynx—an epidemic passed from hare to lynx and a change in lynx trapping activity as a response to the hare cycle: "Trappers might sit out poor years and return to the woods only when the hare again become abundant. Then, once in the field, they could turn a disproportionately large share of their efforts toward catching the more profitable lynx" (p. 729). In commenting on these suggestions, (1) we do not know of any evidence for lynx being subjected to hare epidemic diseases, and (2) although we feel that there probably is a relationship between the hare cycle and lynx trapping, during the late 1800s (the time period from which the data came) it was probably a rare trapper who could afford to sit out poor hare years.

In the discussions of hare-lynx interactions in the literature this latter factor, the relationship of the trapper's strategy for harvesting lynx to the hare's population cycle, seems to have been largely ignored until Gilpin's suggestion. Gilpin's suggestion, however, was made in passing and lacks realism in the way it was phrased. The Hudson Bay Company's fur records have to do with trappers and their harvesting strategies. In fact, in looking for a lynx-hare interaction in these records, investigators were actually looking at a trapper-lynx-hare interaction.

The trapping of fur-bearing mammals remains an important part of the subsistence economies of many northern Canadian Indian and Inuit communities (e.g., Weinstein 1976). Like the lynx, the trapper is an opportunistic predator. The northern hunters have been primarily concerned with obtaining enough food to support their families in the bush and, coincident with this, with trapping fur-bearing mammals as a cash resource. The beaver has been a very valuable resource species for many of these hunters because it provides both relatively large quantities of food per kill as well as pelts. Lynx provide food and furs, but the food returns from a single kill are quite small. If the lynx is a spatially dispersed resource, the hunting effort probably would not justify the time it takes away from hunting more efficiently harvested animals, unless food is very plentiful.

During the years when the hare population is high, there probably is an increase in the lynx population, but considering the lynx's low intrinsic rate of increase it is doubtful if a population increase of the order seen in the fur-return records could follow so closely behind the hare cycle. Rather, it is more probable that hare and lynx hunting are related activities. During years of abundant hare the high availability of food may release more time for trappers to hunt lynx. In addition, lynx preying on hare during these years may concentrate themselves in the vicinity of hare runs. Keith and Meslow (1966) have found evidence of lynx traveling along hare runs. We do not know, however, how this practice varies with the abundance of hares. If the lynx do concentrate around the runways, the trappers could efficiently set lynx snares and traps at the same time that they snare hare for their food. On the other hand, during years when the hare population is low the trappers concentrate on other food resource species, which may take them away from good lynx habitat. If the lynx are also more dispersed at these times they would only occasionally be pursued.

Thus the lynx records of the Hudson Bay Company may not reflect changes in the population density of lynx but short-term changes in the hunting strategy of trappers who sold their pelts to the Bay.

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LITERATURE CITED

Banfield, A. W. F. 1974. The mammals of Canada. University of Toronto Press, Toronto.

Butler, L. 1953. The nature of cycles of populations in Canadian mammals. Can. J. Zool. 31:242–262.

Cole, L. C. 1951. Population cycles and random oscillations. J. Wildlife Manage. 15:233–252.

Gilpin, M. E. 1973. Do hares eat lynx? Amer. Natur. 107:727–730.

Keith, L. B. 1963. Wildlife's ten year cycle. University of Wisconsin Press, Madison.

Keith, L. B., and E. C. Meslow. 1966. Animals using runways in common with snowshoe hares. J. Mammal. 47:541.

Leigh, E. R. 1968. The ecological role of Volterra's equations. Pages 1–61 *in* M. Gerstenhaber, ed. Some mathematical problems in biology. American Mathematical Society, Providence, R.I.

Palmer, E. L. 1957. Palmer's fieldbook of mammals. Dutton, New York.

Weinstein, M. S. 1976. What the land provides; an examination of the Fort George subsistence economy and the possible consequences on it of the James Bay hydroelectric project. Grand Council of the Crees (of Quebec), Montreal.

MARTIN S. WEINSTEIN

RIONDEL, BRITISH COLUMBIA, CANADA V0B 2B0

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