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Predators of cyclic prey: is the Canada lynx victim or profiteer of the snowshoe hare cycle?

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Most populations of predators of cyclic prey fluctuate as their reproductive output and survival is a function of prey availability. The predator's response to a given prey density, however, may alter from the increase to the decrease phase. In cycles, the development of the prey population is predictable, and more sophisticated strategies can evolve. We develop an hypothesis on the life history strategy of the Canada lynx (*Lynx canadensis*). We propose that resident lynx form a core population and occupy large and stable home ranges throughout the cycle. Their reproductive output is maximized with increasing prey availability, but reduced in the decline phase before the investment threatens the long-term survival of the residents.

The population cycles of the snowshoe hare (*Lepus americanus*) and the Canada lynx (*Lynx canadensis*) in the Nearctic boreal forest became a classic textbook example of predator-prey relationship, when MacLulich (1937) and Elton and Nicholson (1942) presented the famous fur harvest data of the Hudson's Bay Company. Though the lynx cycle has often been re-interpreted, a majority of the authors analysing these data have considered the number of lynx to be a function of snowshoe hare abundance. Nobody, so far, has asked the question: what evolutionary adaptations have enabled the Canada lynx to make optimal use of the prey cycles. In this paper, we present an hypothesis on the life history strategy of this predator.

Present knowledge and contradictions

In the last thirty years the lynx fur harvest data have been complemented with field studies. Most of these studies concentrated on years of high lynx abundance and on the decline phase. The lynx population tracks the hare population with a time lag of one or two years (Bulmer 1974, Brand et al. 1976). When the hare popu-

lation crashes, the very abundant lynx face a vanishing food base. To this rapid change, lynx respond through an increase in travel distances and individual home ranges expand (Ward and Krebs 1985). Below a certain threshold density of hares, lynx become nomadic and aggregate in areas where hares are more abundant (Brand et al. 1976, Ward and Krebs 1985). The physical condition of lynx decreases during the decline phase (Parker et al. 1983), leading to reduced reproduction initially by yearling females (Van Zyll de Jong 1963, Brand et al. 1976, O'Connor 1986), and then to an almost complete halt of reproduction by nearly all females (Nellis et al. 1972, Brand et al. 1976). Survival is reduced because young animals starve (Brand et al. 1976, Parker et al. 1983), and vulnerability to trapping increases (Ward and Krebs 1985). The major event in the lynx cycle (and for most individuals the fatal catastrophe in their life) is the crash of the snowshoe hare population. Lynx start to wander and are killed in trappers' snares, or starve to death. This scenario presents the Canada lynx as a victim of the hare cycle, as the healthy lynx population is destroyed through the rapid hare decline.

We studied the Canada lynx in two different areas in the southern Yukon Territory, Canada: one in the Klauane Game Sanctuary, as a part of an ongoing study on the boreal forest ecosystem (Krebs et al. 1992), and the other in the Snafu area, ongoing since 1986 (Slough and Mowat, unpubl.). According to the observations of Ward and Krebs (1985), we hypothesized that the lynx's response to the hare cycle would be a straight function of food availability. We expected that with increasing hare density, lynx reproduction and density would increase, and home-range size would decrease. After the hare crash, we expected to see the reverse response. Home-range size would increase and lynx would start to

become nomadic and leave the area. Females would no longer reproduce after their physical condition became too poor. These predictions did not all prove to be true. We found no change in home range size or overlap between resident neighbours, though the lynx density increased 10–15 fold with increasing hare abundance. Some resident adult lynx emigrated from the study areas before or at the peak hare density, but both female and male yearlings stayed inside the parental home ranges after the hare crash. Lynx showed drastically reduced reproduction in summer 1991 in the Kluane area and one year later in the Snafu area. Nevertheless, the physical condition of the lynx remained good. Females which had not successfully reproduced showed very high body fat deposits.

The core population

From these observations, we felt that the resident lynx we had observed in the study areas were adopting an alternative strategy to emigration and death, namely that of remaining resident and not breeding through the low of the cycle. Brand et al. (1976) had already observed through snow tracking, that lynx home range size was not correlated with either lynx or hare density. Resident lynx seemed to be territorial, though this obviously did not act as a density-limiting mechanism. We think that Brand and co-workers followed – as we did in our recent studies – members of a stable “core population”, which form a K-selected nucleus within the lynx population, and have adopted a specific life history strategy in regard to the cyclic prey.

Many species are confronted with fluctuating food resources. The two alternative strategies that can be applied in such a situation are (1) to behave conservatively and adapt to the low level of food availability, or (2) to become an r-strategist with the ability to react to a sudden increase in prey. However, if the fluctuations are cyclic, and therefore the change in prey abundance become predictable, a more sophisticated strategy can evolve. Though other mammalian predators and raptors in the boreal forest ecosystem might cycle as well (Bulmer 1974), the lynx is the most prominent example to demonstrate such a strategy. The amplitude of the lynx population cycle is higher than that of any other predator (Bulmer 1974). This indicates that the lynx makes extensive use of the hare increase, but that alternative prey to maintain a high lynx density after the hare population crash is not available. From the strong fluctuation in density, the lynx appears to be a classic r-strategist. However, the Canada lynx is a member of the cat family which is a typically K-selected carnivore group (review in Eisenberg 1986). The adaptation to the cyclic snowshoe hare as the main prey probably started only in the late Pleistocene or early Holocene (Breitenmoser and Breitenmoser-Würsten, unpubl.), and we can suppose

that at the beginning of this adaptive process, the Canada lynx showed a more cat-like demography with low density and low reproduction, as it still does at the southern edge of its area, where the population does not cycle (Brittell et al. 1989, Koehler 1990). Some morphological adaptations for hunting small prey (hares) in deep snow, such as larger paws and reduced weight, are obvious differences from the closely related Eurasian lynx (*Lynx lynx*). But what life history strategy could an individual lynx adopt to increase its fitness when it is facing a cyclic prey population?

Individuals in the cycle

First, individual survival is important. A lynx can live long enough to survive through two 10-year cycles. In the Snafu area, eight lynx (two males, six females), born before the 1981 peak, were followed through the 1990 hare peak. In the Kluane study site, one male had occupied the same home range for at least ten years and had survived two peaks. A lynx which manages to survive the lean years could take advantage of high reproduction during two hare peaks, while saving energy but ceasing reproduction during the low. This is the K-strategy for long term survival. A lynx applying such a strategy should maintain a constant territory during the whole cycle. It would be a poor strategy to reduce the occupied territory with increasing hare abundance, then to compete with other lynx for remaining patches of prey during the decline, or to be forced into transiency, and eventually face starvation.

Second, a lynx must maximize its reproductive output when food is abundant. All members of a population compete for their contribution of genes to the following generations, and as this is partly a function of reproductive output, self-restriction should not be an evolutionary stable strategy. The potential reproduction of the Canada lynx is unique in the cat family. In peak hare years, a female can have up to eight kittens which survive the winter (M. Fuller, pers. comm.). In this period, ten-month-old females also reproduce. Repeated copulation with several males as the lynx density increases could induce a higher ovulation rate. The high reproductive output does not depend only on high food availability. Experiments with well-fed Canada lynx in fur farms have not produced the same high litter size, and female yearlings rarely bred (T. Stanfield, pers. comm.). On the one hand, an individual should produce offspring for the next generation, and all should disperse. On the other hand, if an individual is forced to share its once exclusive home range with conspecifics through increasing population pressure, it would do better to share its range with its own progeny. The adequate tactic to satisfy both needs would be a sex biased dispersal. We have observed that male offspring

left their natal range, whereas young females were more likely to remain in their mothers' home ranges.

Finally, when the prey population starts to decline, the reproductive arms race must be stopped before it threatens the expected profit. There should be a threshold prey density at which it no longer pays to invest in further reproduction, but instead pays to share the decreasing food resource with relatives (e.g. yearling offspring). This threshold food density should be above the starvation level. In summer 1991 and winter 1991/92, one year after the hare peak, yearling lynx of both sexes (born in 1990) in the two study areas still remained in their mothers' home ranges. We observed a yearling male, his mother, an adult male, and an unknown lynx travelling together throughout the winter 1991/92 in the Klauane area.

Conclusions and predictions

Our "core population hypothesis" implies that, in the Canada lynx, a small part of the population behaves conservatively, maintaining, as residents, stable territories throughout the cycle. This core population shows the same typical spatial organization described for other felids. The resident lynx increase their reproductive output with the increasing hare abundance. Male offspring disperse during the increase phase, which leads to enhanced competition between resident and transient males for mates and territories. Female offspring, however, stay within the parental home ranges. This leads to increasingly overlapping home ranges of closely-related females and finally to female kin-clusters. The high degree of relatedness among philopatric females could even increase the reproductive output, as proposed by Lambin and Krebs (1991) for fluctuating vole or lemming populations. Close-related females are assumed to be tolerant of each other, predisposed to share space and food. This could be especially important in late spring, when lynx breed, and prey is relatively scarce, even during the increase phase.

After the hare crash, both female and male yearlings are tolerated in the parental home ranges. As females no longer reproduce, the competition among males for mates vanishes, and young males no longer gain a reproductive advantage from dispersing. The result is increasing competition between parents and offspring, and an increasing likelihood that a resident lynx's territory will be taken over by a close relative. The takeover need not be aggressive. Though lynx can survive two hare cycles, they probably cannot make it through three peaks. Hence, after each crash, half the residents should be replaced. Our hypothesis focuses on the territory as a key resource.

From our core population hypothesis, we derive the following predictions for the Canada lynx: (1) The territories occupied by residents at the cyclic low are main-

tained throughout the cycle. During the phase of increasing hare density, they will be shared with a number of female offspring, and during the peak and decline also with male kin. (2) During years of decreasing food availability, survival of lynx owning a territory is higher than that of transients. (3) Young females stay and reproduce inside or close to their mothers' territories. Thus, females with overlapping home ranges are closely related (mother-daughter or sisters), and, therefore, tolerant of each other. Reproductive output is higher at a given hare density during the increase phase than at the same density in the decline. (4) Male offspring disperse during the increase and peak phase and try to take over a territory or to have temporary access to mates. Resident males are intolerant of other males. In the decline phase, young males also stay in the parental home ranges.

To test these predictions, we need data on (1) long term spatial behaviour of lynx, (2) relatedness of neighbouring individuals, and (3) (inclusive) fitness of lynx of different social status. The fates of territorial and transient individuals need to be followed throughout the cycle in an unharvested area, as trapping produces a sex and age biased loss in a lynx population (Quinn and Thompson 1985) that is likely to obscure any social mechanism. When dealing with life history strategies, the quality of data is crucial. Although there is a longer observation series and more data available for the Canada lynx than for most other felid predators, our understanding of the social factors involved in the cycle is rudimentary. No study so far has provided the detailed information needed.

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