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Do Hares Eat Lynx?

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LETTER TO THE EDITORS

DO HARES EAT LYNX?

To test a recently developed predator-prey model against reality, I chose the well-known Canadian hare-lynx system. A measure of the state of this system for the last 200-odd years is available in the fur catch records of the Hudson Bay Company (MacLulich 1937; Elton and Nicholson 1942). Although the accuracy of these data is questionable (see Elton and Nicholson 1942 for a full discussion), they represent the only long-term population record available to ecologists.

The model I tested is

$$dH/dt = H(r_H + C_{HL}L + S_HH + I_HH^2), \quad (1a)$$

$$dL/dt = L(r_L + C_{LH}H + S_LL + I_LL^2), \quad (1b)$$

where L and H are state variables that measure, respectively, the densities of the lynx and hare populations. The parameters have the following significance: the r 's ($r_H > 0$ and $r_L < 0$) are low-density single-species growth rates; the C 's ($C_{HL} < 0$ and $C_{LH} > 0$) are interspecies coupling constants; the S 's are intraspecific social interactions ($S > 0$ is cooperation and $S < 0$ is disoperation); and the I 's (< 0) are intraspecific interference.

To perform the test, the derivatives in equations (1a) and (1b) were approximated by the per year changes in lynx and hare densities. Next, the parameters in these equations were adjusted so that the sum of the squares of the error between the observed growth rate and the predicted growth rate (that is, the right-hand sides of eqq. [1a] and [1b] with the observed initial values substituted for L and H) is minimized.

The methodology and philosophy of this approach are fully explained by Ayala, Gilpin, and Ehrenfeld (1973). The idea is not to explain away a real phenomenon. Rather, it is to test the generality and efficiency of a theoretical model. The correlation between the model and the empirical data gives some idea about the general worth of the model. The level of significance of the individual parameters indicates the efficiency of the model. If a model satisfies both of these requirements, and if the parameters have a plausible biological interpretation, then the model may be useful for suggesting additional observations or experimental manipulations. Furthermore, the model would be expected to be of some relevance to similar ecological systems.

To test my model, I used some lynx-hare population data that Leigh (1968) tabulated; these data run from 1847 to 1903. He used these data to

test the Lotka-Volterra model of predation, which is equations (1a) and (1b) with the S and I values set identically equal to zero. His fit was poor. And since he also showed that over this 56-year period the peak lynx abundance occurred, on the average, a year before the peak hare abundance, he concluded that the lynx-hare oscillation was not a predator-prey oscillation (i.e., a neutrally stable Lotka-Volterra oscillation).

Since my model has greater flexibility than the Lotka-Volterra model and permits, for instance, stable limit cycle oscillations, I felt that it might fit the data better. But the regression fit was equally poor. In fact, it was worse than poor; it was impossibly bad. The signs of the interspecies coupling constants were reversed. Mathematically, the hare was the predator.

To help me understand this, I used graphical predation theory (Rosenzweig and MacArthur 1963) to analyze the system. I plotted the data on the lynx-hare phase plane. The last three 10-year oscillations were very revealing (fig. 1). When the prey is plotted on the abscissa and the predator on the ordinate, any oscillations must run counterclockwise. In other words, the phase of the predator oscillation should be delayed behind the phase of the prey oscillation. As is clear from figure 1, the overall tendency of these three oscillations is clockwise. While other 10-year lynx-hare oscillations have the expected phase relationship, the existence of this anomalous relationship over a 30-year period is curious and stimulates efforts toward its comprehension.

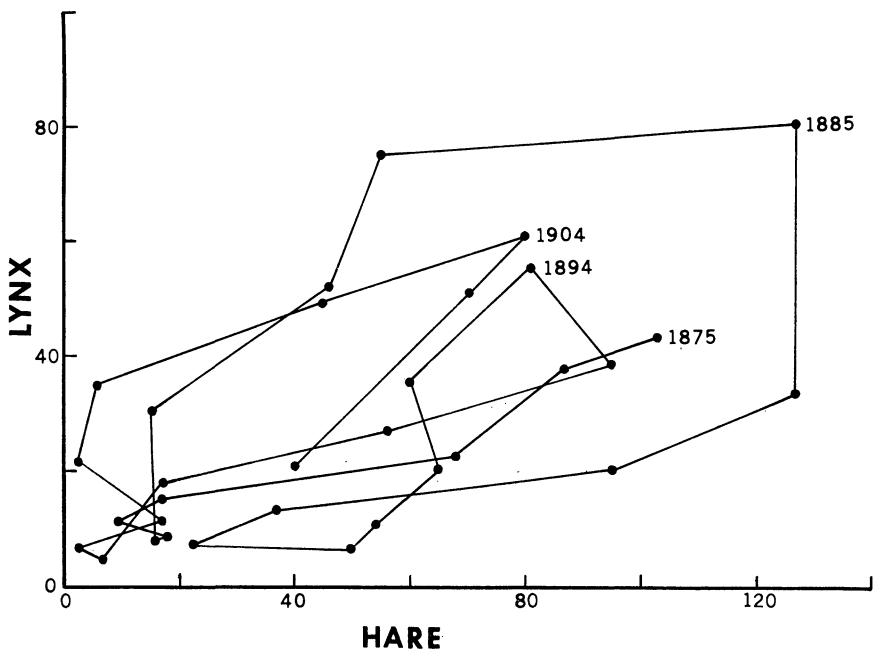


Fig. 1.—Yearly states of the Canadian lynx-hare system from 1875 to 1906. The numbers on the axes represent the numbers of the respective animals in thousands.

Some have suggested (e.g., Lack 1954) that the cause of the oscillation lies in the relationship of the hare to its food. And Keith (1963) has shown that on certain islands hares oscillate in the absence of lynx. A realistic model of the lynx population, then, would be that it depends on a time-varying carrying capacity, that is, the level of its food resource, the hare population. This is mathematically formulated as follows:

$$dL/dt = \frac{rL}{K(t)} [K(t) - L], \quad (2)$$

where r is an intrinsic growth rate and $K(t)$ is proportional to the hare population density. Analysis of this model shows that the phase of lynx population oscillations must lag behind the phase of externally produced hare population oscillations. Thus, the nature of the oscillations in figure 1 remains unexplained.

The oscillations in figure 1 are "figure eights." If the small loops near the origin are ignored, the oscillations conform to graphical predation theory (Rosenzweig and MacArthur 1963), with the hare assumed to "eat," or prey upon, the lynx. It is, of course, nonsense to assume that hares actually eat lynx. Nonetheless, an abundance of hares could indirectly kill lynx by vectoring a disease to them.

To test this theoretical possibility, I constructed a computer model in which a classical epidemic (see Watt 1968) passes through the hare population when a certain threshold density of hares is reached. The epidemic is assumed to be nonfatal to the hares, but the interaction between lynx and diseased hares causes a certain percentage mortality to the lynx. By postulating a disease reservoir, requiring the hares to oscillate sinusoidally and adjusting other parameters in a not unreasonable manner, I was able to obtain "figure eight" oscillations that resembled those in figure 1.

Chitty (1948) observed an epidemic in a hare population when it was increasing and near one of its 10-year peaks. This is a possible candidate for the proposed pathogenic organism. But several associates who read an earlier draft of this letter suggested a more probable candidate: *Homo sapiens*, the ecological race Canadian trappers. Trappers might sit out poor years and return to the woods only when the hare again became abundant. Then, once in the field, they could turn a disproportionately large share of their efforts toward catching the more profitable lynx.

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