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CYCLES IN CANADIAN LYNX

Because of the confusion which often seems to surround studies of population cycles, and because we are still trying to understand what these cycles represent, it is necessary to be particularly cautious when examining data series, especially when comparing one series to another. A good case in point is a challenging paper (Gilpin 1973) purporting to demonstrate that the lynx pelt cycle, instead of following the cycle in snowshoe hare as one would expect for a predator-prey cycle, is actually sometimes ahead of the hare cycle. Gilpin's paper and a more recent commentary (Weinstein 1977) suggest that the fur trappers might be a major pressure on the population and that the cycle in lynx might reflect hunting strategy changes among trappers rather than changes in the population density of lynx.

The phenomenon is in fact an artifact created by comparing data which are not comparable. The data being compared are from a paper describing the ecological role of Volterra's equations (Leigh 1968). The data were coarsely estimated, as Leigh clearly states, from a graph comparing hare and lynx fluctuations (MacLulich 1937); the coarseness can be appreciated by referring to the original data (MacLulich 1957, snowshoe hare; Elton and Nicholson 1942*b*, lynx). The hare data are from the Hudson's Bay Company records for the area around James Bay, the southern end of Hudson's Bay in eastern Canada. The lynx data represent Hudson's Bay fur returns for all of Canada. Elton and Nicholson (1942*b*) painstakingly separated the lynx returns into separate geographical regions, and one can clearly see that the bulk of the pelts derived from central and central western Canada. (The series of lynx pelts for the James Bay area is unfortunately too incomplete to be usefully compared to the hare.) Thus the comparison is essentially between rabbits from eastern Canada and lynx from western Canada.

Several points can be clarified by understanding the sources of the data. Elton and Nicholson (1942*b*) found evidence for a trend in peaks in lynx outwards from the Athabasca basin (north Saskatchewan) indicating that the cycle is not synchronous over the whole of Canada and takes typically 1-2 yr to spread to the southern shore of James Bay (Williamson 1975). One cannot clearly assess what the phase difference between lynx and hare would be for a single locale without actual data for that locale, so it would be merely speculative to say that hare precedes lynx, or vice versa. Additionally, it has been suggested (Finerty 1971) that the period length of the average rabbit cycle in James Bay may be slightly greater than the length of the average lynx cycle in the Mackenzie River District (central western Northwest Territories). This appears to explain what is observed when graphical predation theory is used on these lynx and hare data. The predator oscillation appears to begin behind the prey oscillation, and this relationship gradually reverses (Gilpin 1973). Because of the geographical discrepancies these two series cannot be compared to test the validity of the theoretical model. It can be seen, however, that these apparent anomalies support the ideas that the cycles are not exactly synchronous over large areas and that it is possible, although as yet insufficiently documented, that period lengths of cycles may vary in different areas.

Another important factor (Gilpin 1973; Weinstein 1977) is that when hares are abundant, providing easily obtainable food for the basically subsistence economies of

many north Canadian Indian communities, trappers may have more time to trap valuable furs for trade. If hare predators tend to concentrate near hare runs (Weinstein 1977), the trapper may more efficiently trap hare and lynx for both food and valuable furs. In years of low hare abundance, trappers might move from habitats suitable for hare predators, causing the predator population figures (estimated from fur returns) to appear to drop more rapidly than the actual fact. Although this might enhance population peaks and troughs, it is not clear how it would generate regular periodicity. If the hare were cycling, and the lynx fur returns therefore appeared to cycle because the trappers were catching lynx incidentally in their search for food, it is possible that the lynx might not actually cycle (Weinstein 1977). The lynx, however, have not been properly sampled for assessing this. Moreover many naturalists have noted the abundance of lynx in peak years (Elton and Nicholson 1942*b*) and the magnitude of the lynx cycle seems too great to be explained by this trapper process. Also, the existence of periodicities in at least one other predator-prey pair, mink and muskrat (Elton and Nicholson 1942*a*; Bulmer 1974), plus cycles in several other mammal species (Finerty 1971; Bulmer 1974) probably could not be explained in a similar fashion.

Weinstein (1977) suggests that the biology of the lynx may not be able to explain the dramatic increases seen in the pelt records. It might be true that these occasional large rates of increase could not be explained by asserting that the lynx cycle is following hare abundance in a given area. However, the wide variation in phasing of peaks in the lynx cycles, (suggesting an outward spread of lynx abundance from a central area [Elton and Nicholson 1942*b*; Butler 1953]) implies that the lynx may be emigrating to follow the rabbit resources, and this could account for what is observed. Additionally, the average lynx litter size is two to three kittens, with a range as high as five kittens, with one litter per year (Banfield 1974). Examining the distribution of the change in number of lynx pelts for the Mackenzie River District, Williamson (1972) observed that on the upswing the average rate of population increase doubles. Females mature in their first year and, allowing for a single annual breeding season, the rate of the population increase would be equal to parental survival plus the product of the proportion of females born and the rate of juvenile survival (E. L. Charnov, personal communication). If food is abundant so that parental and juvenile survival are high, a female birth rate of slightly more than unity might be sufficient to double the population annually. Emigration from an epicenter (Butler 1953; Watt 1968) might account for yet higher population growth rates, or compensate for discrepancies due to nonbreeding females. Thus the biology of the lynx could allow for the increases observed.

While none of these suggestions is thoroughly enough documented to make definitive statements it seems premature to abandon the possibility that lynx cycles may actually exist.

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GLOBAL STABILITY OF FOOD CHAINS

Goh (1977) has shown that if a generalized Lotka-Volterra model for n interacting species

$$\frac{dN_i}{dt} = N_i \left(b_i + \sum_{j=1}^n a_{ij} N_j \right), \quad i = 1, \dots, n, \quad (1)$$

has a nontrivial equilibrium $\bar{N} = (\bar{N}_1, \bar{N}_2, \dots, \bar{N}_n)$ with each $\bar{N}_i > 0$, then the Lyapunov function

$$V(N) = \sum_{i=1}^n c_i \left[N_i - \bar{N}_i - \bar{N}_i \ln \frac{N_i}{\bar{N}_i} \right] \quad (2)$$

has a time derivative given by

$$\frac{dV}{dt} = \frac{1}{2} (N - \bar{N})^T (A^T C + CA) (N - \bar{N}), \quad (3)$$

where $C = \text{diag} [c_1, c_2, \dots, c_n]$ and $A = [a_{ij}]$. Hence the equilibrium point \bar{N} is globally asymptotically stable (i.e., the domain of attraction of \bar{N} is the entire positive orthant) if there is a diagonal matrix C such that $A^T C + CA$ is negative definite.

It should be pointed out that the Lyapunov function (2) has a long history of application to Lotka-Volterra models. It was used by Kerner (1957) as a constant of motion when $A^T C + CA = 0$, and by Huang and Morowitz (1972) and Aiken and Lapidus (1973) to show asymptotic stability when $A^T C + CA$ is a negative diagonal matrix. Walter (1974) used $k_1 \exp(V) + k_2$ to show global stability of a one-predator-one-prey system, and Harte and Levy (1974) used V to study domains of attraction for systems that are similar to (1). I (Harrison 1975) used V to arrive independently at the same conclusion as Goh. Goh (1976) gave the result for two