



Snowshoe Hare Populations: Squeezed from Below and Above

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vinyl monomers and their derivatives. In hindsight, the concept outlined by Fréchet is relatively simple. In principle, this new polymerization method is quite versatile as it should be compatible with the wide range of chemistries associated with vinyl monomer polymerizations, although this first report (1) is focused on cationic processes. The method involves the activation of an AB vinyl monomer by an external stimulus, which in this case involved the addition of a Lewis acid to the monomer, which generates a B* moiety that is capable of initiating the polymerization of a vinyl monomer (Fig. 2). The self-condensing then begins with the addition of the B* moiety across the double bond of another AB* monomer unit to afford a dimer that contains one conventional propagating center and one B* center capable of further initiation. At this stage, this dimer now contains two active centers possessing essentially equivalent reactivities and one double bond. As such, this AB monomer has now been transformed into an AB₂-type monomer, which is known to give rise to hyperbranched "dendritic" polymers. Subsequent condensations lead to highly branched polymeric materials with high molecular weights through simple vinyl additions.

Considering the universality of self-condensing vinyl polymerizations, it will not be long before we see a plethora of new materials based on this innovative achievement. It should not be too difficult to extrapolate to such new materials as dendritic perfluoropolymers, liquid crystalline polymers based on simple vinyl monomers (9), thermoplastic elastomers, and perhaps even a new version of PE.

The challenges that now remain include the extension of this work to mechanisms other than propagating carbocations, such as radicals; the use of light and thermal energy as external stimuli; the development of synthetic methodologies for the creation of new "self-condensing" monomers from other readily available monomers; and the creative combination of "self-condensing" monomers with conventional monomers to generate unique materials with significantly new properties.

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All ecologists favor long-term studies and in this respect differ from chemists, physicists, most other biologists, and all politicians. But, like other scientists, ecologists prefer to do experimental work. ... We must combine these two approaches to solve the major ecological questions (1, p. 3).

The cyclical population density of the Canadian snowshoe hare (*Lepus americanus*), with high densities occurring every 9 to 11 years, is a classic example of the multiannual cycles in many vertebrate populations of the boreal zone (2–4). Although the cycles in the hare population are cited in almost all introductory biology texts, their cause has been obscure. Food, predators, disease, and sunspots have all been put forward as essential, but there has been no agreement as to which factors best explain the cycles. Now, Krebs and his co-workers, on pages 1112 to 1115 of this issue (5), report a technically unique and important experiment indicating that the hare population cycle results from a food-hare-predator interaction.

The new results show that the effects of food and predation on population density are nonadditive. Food augmentation and exclusion of mammalian predators separately caused about a twofold increase in the abundance of individual hares, whereas combined addition of food and reduction of predation increased the population density by a factor of 10. Krebs and co-workers therefore argue that neither plant-herbivore nor predator-prey interactions are by themselves sufficient for cycling. Although this notion is consistent with the earlier suggestion of Keith (4) that the periodic fluctuations in the hare population are due to a dynamic interaction between predators and food shortage during winter, the new results do not necessarily support Keith's proposed sequential two-level interaction that assumes food shortage to be temporarily followed by predation.

The validity of the proposed three-trophic-level hypothesis may be tested independently by examining long-term monitoring data of snowshoe hare populations (6). If a three-level interaction is truly responsible for generating and maintaining

the observed dynamics, the relevant time series should exhibit dimension (7) three or higher. Indeed, the structure of the hare time series is consistent with dimension three (8) and is therefore consistent with the proposed three-level hypothesis. In theory, a three-dimensional structure in the time series could also arise because of several other three-factorial explanations; however, the extraordinary consistency between the experimental and the time-series data greatly strengthens the plant-hare-predator hypothesis. This consistency is emphasized by the facts that (i) the experimental and the time series data are independent sources of information; (ii) by combining these two data sources, insights derived from experimental manipulation can reinforce insights from statistical analyses of observed patterns; and (iii) the new experimental results allow a biological interpretation of the estimated dimensional structure of the time series.

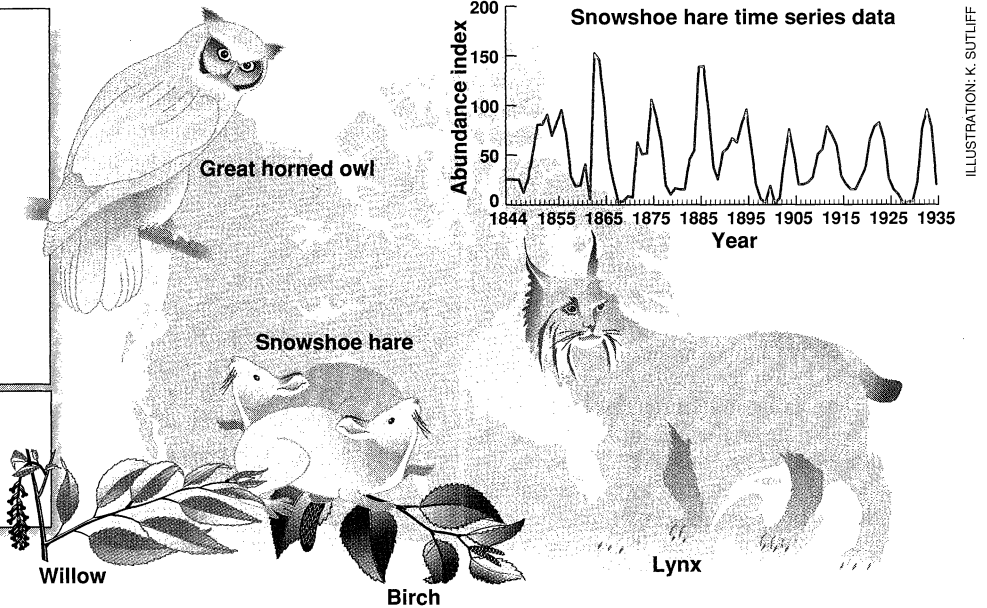
Indeed, this synthesis is an example of the integrated, dual approach to ecology advocated by Krebs in 1991 (1). I agree with Krebs (1, p. 3) that "monitoring of populations is politically attractive but ecologically banal unless it is coupled with experimental work to understand the mechanisms behind system changes." Further, the utility of experimentally deduced mechanisms, like the new work of Krebs *et al.* (5), is greatly enhanced if these mechanisms can be shown, as I have attempted above, to generate the patterns they are supposed to explain.

Many Northern microtines—lemmings and voles—also exhibit periodic fluctuations in their population densities (10). The estimated dimension of the time series for small rodents is typically two (11), suggesting that the microtine cycle may be caused by fewer processes than are involved in the snowshoe hare cycle. Krebs favors a structurally simpler hypothesis—the so-called Chitty hypothesis (12)—for the microtine cycle, consistent with the estimated lower dimensionality of the microtine time series. This hypothesis assumes that some population-intrinsic factor by itself causes the density cycle. But much experimental and theoretical evidence suggests that the Chitty hypothesis cannot explain the cycle (10, pp. 70–73); extrinsic factors also seem essential (10, 13). Perhaps

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A The Krebs <i>et al.</i> experiment		
Treatment I Reducing predators	Treatment II Adding food	Treatment I & II Combined experiment
$-P_t$		$-P_t$
2x increase in H_t	2x increase in H_t	10x increase in H_t
	$+V_t$	$+V_t$

B Statistical model
$h_{t+1} = \alpha_0 + \alpha_1 h_t + \alpha_2 h_{t-1} + \alpha_3 h_{t-2} + \epsilon$



Understanding population dynamics by combining experimental and modeling approaches. The structure and dynamics of ecological systems (such as the snowshoe hare of the Canadian boreal forest) may be deduced through a pluralistic approach. **(A)** Experimental manipulations like those reported by Krebs *et al.* in this issue of *Science* (5). Assuming H_t to be the abundance of the hare at time t , the statistical modeling has been done using $h_t = \ln[H_t]$. **(B)** Statistical modeling of long-term data (6, 8) [as well as mathematical modeling (7)]. The snowshoe hare cycle may result from a dynamic interaction between the food supply of the hares

[willow (*Salix glauca*) and birch (*Betula glandulosa*)], the hares, and the mammalian predators on the hares [lynx (*Lynx canadensis*), coyote (*Canis latrans*), and great horned owls (*Buteo virginianus*)] (9). If the food supply, the hare population (h), and the predators each can be modeled as one entity, a system of three difference equations is a plausible mathematical description of the system, implying an expected three-dimensional structure of long-term time series data on the hare, which in fact is observed (8). [In the statistical modeling $h_t = \ln(H_t)$ has been used as the transformed variable in the analysis.]

either food or predators may be responsible for the microtine cycle, accounting for the estimated dimensionality of two of the small rodent time series. This two-trophic-level hypothesis for microtines awaits experimental testing, such as has now been provided for the snowshoe hare.

The hare cycle and the microtine cycle will continue to fascinate ecologists as they have since Elton's classic 1924 paper (2). Thanks to the new study by the Krebs team, ecologists are now able to pose their questions more sharply, and some pieces in the jigsaw puzzle are falling into place.

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- Data from 1844 to 1904 are from the Hudson Bay Company fur records; those from 1905 to 1935 are from trapper questionnaires; both sets are from D. A. MacLulich [*Fluctuations in the Numbers of the Varying Hare (Lepus americanus)*] (Univ. of Toronto Press, Toronto, 1937) and A. R. E. Sinclair *et al.* [*Am. Nat.* **141**, 173 (1993)]. This combined time series is from a different location than the data used for the experimental study in (5), but because the snowshoe hare cycles are synchronized throughout most of the Canadian boreal forest, the two sets of data are assumed to represent the same general phenomena [(4); A. R. E. Sinclair *et al.*, *Am. Nat.* **141**, 173 (1993)], but see C. H. Smith, *Can. Field Nat.* **97**, 151 (1983)].
- This refers to the embedding dimension [B. Cheng and H. Tong, *Philos. Trans. R. Soc. London Ser. A* **348**, 325 (1994); P. Turchin and J. A. Millstein, *EcoDyn/RSM: Response Surface Modelling of Nonlinear Ecological Dynamics* (Applied Biomathematics, New York, 1994)] and represents the number of lags d needed to describe the dynamics with a model $N_{t+d} = N_t \exp[f(N_t, N_{t-1}, \dots, N_{t-d}) + \epsilon]$ [T. Royama, *Analytical Population Dynamics* (Chapman & Hall, London, 1992); *Ecol. Monogr.* **51**, 473 (1981)], where f is some appropriate (linear or nonlinear) function, N_t is the abundance at time t , and $\{\epsilon\}$ is a sequence of martingale differences with constant variance (and is assumed to represent the environmental stochasticity [D. Goodman, *Viable Populations for Conservation*, M. E. Soul, Ed. (Sinauer, Sunderland, MA, 1987), p. 11]). If the underlying dynamics are linear, a model with k factors (for example, k trophic levels) will result in an embedding dimension k . If the dynamics are highly nonlinear, the embedding dimension may be higher, but not lower, than k [D. S. Broomhead and R. Jones, *Proc. R. Soc. London Ser. A* **423**, 103 (1989)]. Many mechanisms other than k trophic interactions can cause lagged dynamics and an embedding dimension of order k ; the process implies the dimension, but the dimension does not imply the process.
- N. C. Stenseth, O. Bjørnstad, W. Falck, unpublished results. We have analyzed the hare time series (6) both as one 92-year-long time series and as two separate time series; both analyses provide analogous results. Details for the combined time series are as follows: The dimension of the square root-transformed time series was estimated by cross-validation with (i) a linear autoregressive model, and (ii) a nonparametric kernel autoregressive model. In (i), maximum likelihood estimates were calculated with a Kalman filter applied to the state space representation of the likelihood [R. Kohn and C.F. Ansley, *J. Am. Stat. Assoc.* **81**, 751 (1986)]. In (ii), nonparametric conditional means were calculated with a Gaussian product kernel (7). The optimal dimension was five for both methods. However, that dimension gave only marginally better predictions (<0.4 percent units) than that of dimension three. Models of dimension two were inferior in either case (by >3.5 percent units). The result is analogous to that obtained with standard information theoretic approximations based on Akaike information criterion [C. M. Hurvich and C.-L. Tsai, *Biometrika* **76**, 297 (1989)]. Tests for nonlinearity were also carried out. The null hypothesis of linearity could not be rejected. A hypothesis of three trophic interactions responsible for the most of the population dynamics is consistent with the time series data: Components of the various trophic levels presumably contribute marginally to the overall dynamics of the snowshoe hare population.
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