Can seasonal changes in density dependence drive population cycles?

Less than two years ago, Charles Krebs[1] called attention in *TREE* to a veritable gold mine of data on the population dynamics of the grey-sided vole, *Clethrionomys rufocanus*, on Hokkaido Island, Japan. This dataset, which was gathered by Japanese foresters because of serious damage to young conifers caused by voles, is the most extensive known for arvicoline rodents (lemmings and voles). Trappers used the same census techniques at 225 sites scattered across the whole island to produce annual estimates of population abundance for 12–31 consecutive years, depending on the site. In 1996–1997, a team of Norwegian and Japanese investigators published several analyses of a subset of these data for 31 years at 90 sites in northern Hokkaido[2–4].

These analyses found strong evidence of direct density dependence in the growth rates of nearly all populations and delayed density dependence in many of them. A geographic gradient occurred with greater amplitude of fluctuations and increasing incidence of delayed density dependence moving from northwestern populations to northeastern populations. This pattern corresponded with a greater propensity for population cycles in the northeast. Now, *Researches in Population Biology* has published a special feature[5] that presents a more extensive analysis of data on the population ecology of *C. rufocanus*. It shows that substantial progress has been made in providing an explanation for geographic gradients in population dynamics across all of Hokkaido.

The special feature begins with a plea for a pluralistic approach to population ecology, so that theoretical developments, including statistical and mathematical modeling, are integrated with the observational and experimental studies needed to test explanatory hypotheses[6]. This paper sets the stage for those that follow, including the following: a review of the systematics of *Clethrionomys* in general and the ecology of *C. rufocanus* on Hokkaido in particular; two reports on social organization and kinship in this species; an analysis of prevalence of parasitic tapeworms in foxes and their relationship to the abundance of voles (the intermediate host); and four papers on statistical and mathematical models of population dynamics and demography. Here, I concentrate on the developments in quantitative analysis summarized by the last four papers.

To analyse the geographic patterns in population dynamics, Saitoh *et al.*[7] divide the 225 time series into 11 groups of 8 to 31 series for different regions of Hokkaido based upon topography. Figure 1 shows the average time series for the 11 regions based on autumn densities near the end of the breeding season. Using several standard techniques, each population is analysed for direct and delayed density dependence. Then the relative strength of the two forms of density dependence is assessed using a second order log-linear autoregressive model:

$$\ln(N_t/N_{t-1}) = b_0 + b_1x_{t-1} + b_2x_{t-2} + e_t$$

where N_t and N_{t-1} are population size at time t and t−1; x_{t-1} and x_{t-2} are the log-transformed abundance at time t−1 and t−2; b_0 is a scaling parameter; b_1 and b_2 are the first and second order autoregressive coefficients for 1-year and 2-year time lags, respectively; and e_t is random noise.

Most populations, except for the southernmost ones, display direct density-dependent population growth, but only in the north and east are there many populations with delayed density-dependent growth. Using estimates of spectral density functions and functional data analysis, Bjørnstad *et al.*[8] find an increasing frequency of cyclic dynamics within a 3.5 to 4.5 year range moving from southwest to northeast across Hokkaido. Thus, these two studies identify a clear and consistent pattern of increasing frequency of delayed density dependence and of cyclic population dynamics moving from southwest to northeast.

To interpret the population gradients, Stenseth *et al.*[9] first note that the most obvious environmental change from southwest to northeast in Hokkaido is the shortening of the growing season, which is also the breeding season for voles. This occurs because of increasing latitude to the north and colder ocean currents on the eastern shores. The authors then propose a mathematical model of population dynamics with direct and delayed density dependence divided into two seasons:

$$N_t = N_{t-1}\exp[(a_{w0} - a_{w1}x_{t-1} - a_{w2}x_{t-2}) \times (1 - \tau)]\exp[(a_{s0} - a_{s1}x_{t-1} - a_{s2}x_{t-2})\tau]$$

where a_0 is the annual maximum rate of population growth; a_1 is the reduction in growth owing to direct density dependence; a_2 is the reduction in growth owing

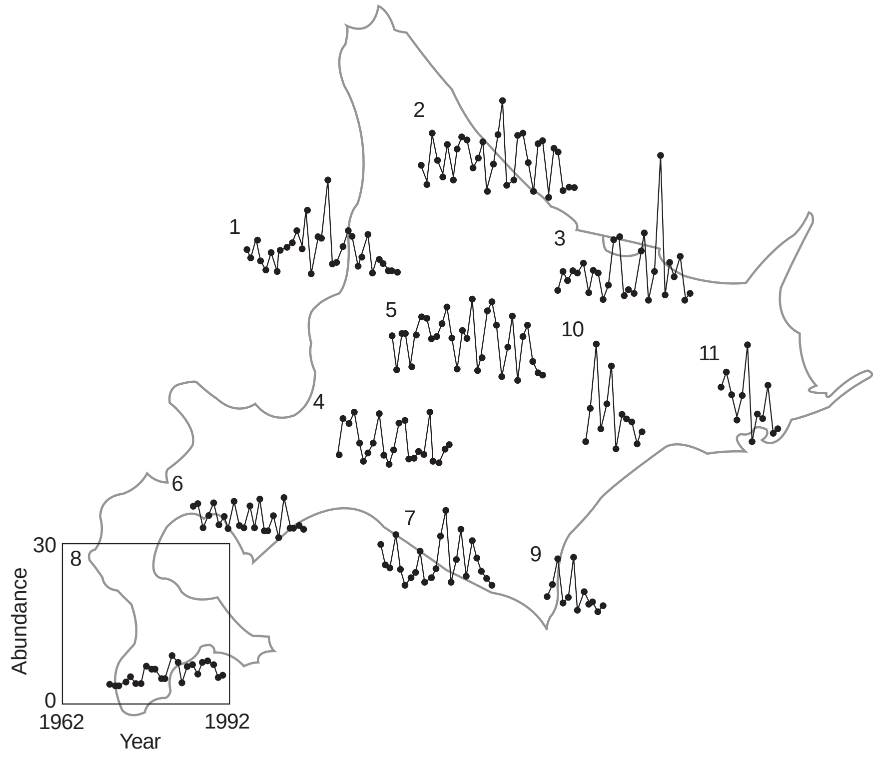

Fig. 1. Average time series for the numbers of grey-sided voles (*Clethrionomys rufocanus*) caught per 150 trap nights are shown for each of 11 topographic regions on Hokkaido Island (Japan). Averages for each region were based on 8–31 sites (a total of 225 time series). All series ended in 1992 and are shown at the same scale, which is given at the lower left for Region 8. *Reproduced, with permission, from Ref. 8.*

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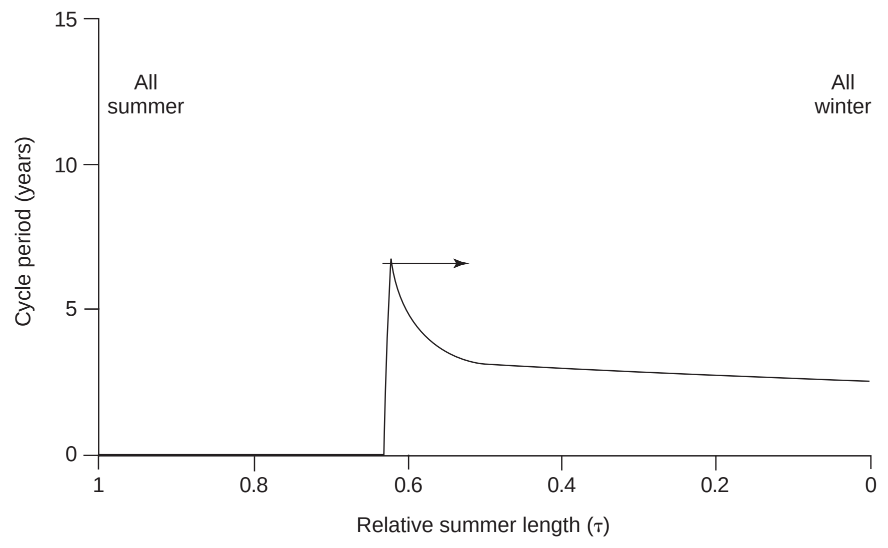

Fig. 2. The effect of changes in length of the growing season (τ) on population dynamics (cycle period) of grey-sided voles (*Clethrionomys rufocanus*) on Hokkaido Island (Japan). Calculations are based on a model of population dynamics for which the strengths of direct and delayed density dependence for summer and winter were estimated from the coefficients of an autoregressive model fitted to each of the time series shown in Fig. 1. The longest growing season (7.5 months, $\tau = 0.63$) occurs in southwest Hokkaido, where population cycles neither occur nor are predicted by the results shown in the figure (cycle period = 0). The shortest growing season (6 months, $\tau = 0.50$) occurs in northeast Hokkaido, where population cycles of 3.5–4.5 years occur, which overlaps with the cycle period predicted by the model. *Reproduced, with permission, from Ref. 9.*

to delayed density dependence; w indicates values for winter; s indicates values for summer; x represents ln$N$; and τ is the length of summer as a proportion of the year. Taking the natural log of both sides of this equation and collecting terms produces an equation analogous to the autoregressive model:

$$\begin{aligned}\ln(N_t/N_{t-1}) &= a_{w0}(1-\tau) + a_{s0}\tau \\ &+ [1 - a_{w1}(1-\tau) - a_{s1}\tau]x_{t-1} \\ &- [a_{w2}(1-\tau) + a_{s2}\tau]x_{t-2}\end{aligned}$$

Now, coefficients (b_t) estimated by the autoregressive model for regions with different values of τ can be used to provide simultaneous equations in the following form for the estimation of the parameters (a_t) in the population model:

$$\begin{aligned}b_0 &= a_{w0}(1-\tau) + a_{s0}\tau \\ b_1 &= 1 - a_{w1} + (a_{w1} - a_{s1})\tau \\ b_2 &= -\, a_{w2} + (a_{w2} - a_{s2})\tau\end{aligned}$$

Predictions of the dynamics implied by these parameter estimates are made using the techniques of Royama[10] and Bjørnstad *et al.*[11] Figure 2 shows the results using the full range of autoregressive coefficients for the average time series of the 11 regions to calculate parameters. The results correspond well with those from the spectral density models; no periodicity is predicted for extreme southwestern populations, where the length of summer averages 7.5 months ($\tau = 0.63$), and three- to four-year cycles are predicted in the northeast, where summer averages six months ($\tau = 0.50$). The model even captures the tendency for longer periods of cycles in geographic regions with intermediate lengths of seasons. This truly remarkable result provides strong evidence that seasonal changes in density dependence could be sufficient to produce the geographical patterns of population cycling observed on Hokkaido.

Using a different approach to population analysis, Yoccoz *et al.*[12] review the statistical models available to analyse mark–recapture data, and apply a series of models to four years of live-trapping data for *C. rufocanus* to estimate survivorship for different cohorts of voles in different seasons and years. Although the data are not sufficient to estimate values very precisely, the authors use suggested patterns in survival and general information on reproduction in a matrix model of population dynamics with different matrices for different seasons. Calculations of elasticities for these matrices indicate that shifts in survival of both young and adults would probably have the greatest impact on population growth. Yoccoz *et al.*[12] suggest that a plausible hypothesis for demographic changes that could cause cycling in *C. rufocanus* would include the following: (1) lower survival during winters following high autumn densities; and (2) lower survival of reproducing adults during spring, and possibly summer, of years with low density.

The good news is that such analyses can provide demographic signatures that allow field workers to test the predictions of various hypotheses regarding the mechanisms of population cycles. The bad news is that statistical models for estimation of survival for different population cohorts, seasons and years require such voluminous data that few mark–recapture studies are likely to be of adequate intensity or scale to provide enough precision, given that an absolute change in survival of only 10% can have a major impact on population growth.

Although producing impressive results, quantitative analyses such as the ones outlined here have their deficiencies. First, the appropriate techniques to be used are still a matter of debate[13,14]. Second, population dynamics within geographical regions are not uniform – more, but not all, of the populations in the north and east show high variability and cyclical dynamics. The causes of variability within regions remain unexplored. Third, as the authors acknowledge, their model of population dynamics is based upon single population estimates each year (autumn density), but they split density dependence into two seasons. This might work well for direct density dependence during winter, which seems likely to be linked to autumn density, but, in summer, populations seem more likely to respond to spring densities. Finally, and also acknowledged by the authors, the seasonal population model is phenomenological and does not implicate any particular mechanism.

No doubt many investigators will be inventive enough to adapt their favorite hypothesis to seasonal change, an exercise that has already begun in an interesting series of commentaries by outside experts at the end of the special feature. These critiques include observations on the differences between the south–north gradient in population dynamics in Fennoscandia compared with the southeast–northwest gradient in Hokkaido[15]; the need to consider ecological interactions and extrinsic factors for the Hokkaido populations (most empirical research to date has focused on issues of social behavior and kinship)[16]; a comparison of the seasonal model for cycles on Hokkaido with seasonal models for other populations, such as measles and Soay sheep[17] (*Ovis aries*, see also *TREE*, January 1999, pp. 1–2); and others that I have no space to mention.

In spite of some reservations, most commentators conclude, and I agree, that the populations on Hokkaido provide a unique opportunity for a major advance in the understanding of population cycles. Because of the incredible effort already expended for monitoring and data analysis that culminated in this special feature, the groundwork has already been laid. Cycling and non-cycling populations have been identified; the geographic pattern of cycling has been linked to seasonal change; several hypotheses have been proposed to account for the pattern; and the editors have provided a summary of studies, mostly empirical, that should have priority[18]. Let the comparative observations and experimental testing begin!

Acknowledgements
While this article was being prepared, the author was supported in part by a grant from the National Science Foundation (DEB 95-28571).

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Sexual selection, speciation and imprinting: separating the sheep from the goats

Most current work on sexual selection and speciation assumes the importance of 'genetically determined' mate preference[1,2]. Males have showy sexual ornaments because females prefer them that way, and females prefer them that way because they are genetically predisposed to do so. But this emphasis on the genetic control of mating preferences flies in the face of a growing body of evidence that mate preferences in mammals[3,4], as well as many birds[1,5], are learned through 'imprinting'.

It has long been known that during early development young birds can learn features of their parents that crucially influence their future mate-choice decisions[5,6]. For instance, Bateson and ten Cate have shown that female quail (*Coturnix coturnix japonica*) and zebra finches (*Taeniopygea guttata*) choose to mate with males that are similar, although not identical, to the parental type[7–9]. Furthermore, these preferences are very often directional, with offspring actually preferring more elaborate ornaments than those of their parents, a feature referred to as 'asymmetrical mating preference' (in contrast to 'parental-type imprinting', in which offspring prefer ornaments to match exactly those of their parents). Surprisingly, little attention has been given to the evolutionary significance of such mechanisms in models of sexual selection, possibly because imprinting has been assumed to be important for only a few bird species. However, sexual imprinting is not only widespread in birds[5]: two new studies, by Kendrick *et al.*[3] and Penn and Potts[4], emphasize the need for a more thorough evaluation by proving that sexual imprinting is also important in mammals.

Kendrick *et al.*[3] have shown that, in accordance with avian studies, young sheep and goats also imprint on their parents. So, although much of their species-specific behaviour is unaffected by cross-fostering, when nanny goats are used as foster parents for male lambs, the lambs grow into rams that prefer goats to sheep as sexual partners. Similarly, when male kids are fostered with ewes, they grow into billygoats that prefer sheep. Kendrick *et al.* suggest that the lambs and kids are imprinting on facial features and basing their mate choice on these visual cues. Superficially, this goes against the widely held view that mammals[10], including humans[11,12], tend to make mate choice decisions based on MHC (major histocompatibility complex) type, which they detect by smell. However, the conflict might not be real, because MHC-based odour preferences can also be learned through imprinting[4].

House mice (*Mus musculus*) show disassortative mating for MHC genes, either by referring to their own odour or that of close relatives[4]. By cross-fostering female mouse pups into MHC-dissimilar families, Penn and Potts[4] have recently shown that females in later life base their mate preference on the MHC genes of their foster family rather than their own MHC genes. This is the first evidence that MHC

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