

Vole cycles on Hokkaido: a time-series goldmine

Many vole populations fluctuate in three- to four-year cycles and much effort and even more argument have gone into studying the causes of these cycles. But even with devoted graduate students and the labours of heroic untenured professors, the scale of studies has been small. This is no longer the case, thanks to the Japanese foresters on the island of Hokkaido.

Voies on Hokkaido are pests, in particular the most common species, *Clethrionomys rufocanus* (the grey-sided vole). Vole damage in forest plantations was widespread in 1937, 1943, 1946 and 1951, and more than one million seedlings in forestry plantations were commonly killed in each outbreak. In 1954 the Forestry Agency of the Japanese government began regular censuses of voles for management purposes on 1000 areas all over Hokkaido. Snap-trapping was done every spring, summer and fall with 50 traps on 0.5 ha grids

for 3–5 nights. In keeping with the best tradition of management agencies, the data were carefully filed away and forgotten, until Takashi Saitoh discovered the gold mine¹. A fortunate linkage between the Oslo ecology group and Saitoh was forged in 1991, and a series of papers has started to mine the gold in the filing cabinets^{2–4}.

Grey-sided vole populations on Hokkaido illustrate well the problems of trying to distinguish between cyclic and non-cyclic populations of small rodents. Saitoh¹ recognized four types of population fluctuations from relatively stable to highly cyclic. Figure 1 illustrates the extremes of these categories. The Heian population fluctuates strongly with peaks four years apart on average. The Ebishima population fluctuates much less and it is much harder to decide from looking at the densities alone whether there is any significant periodicity. Populations were high

together in 1965 and most of the populations Saitoh¹ studied were high in 1978. But there are years in which many populations are completely out of phase. For years, students of small rodent cycles have been designing elegant experiments for out-of-phase populations and Hokkaido has a panoply of them – another gold mine waiting for exploitation.

Population ecology has two broad traditions of study: the time-series tradition (watch-and-count, wait-and-hope) and the experimental tradition (muck-about-with-something). The Hokkaido data analyzed so far consist of 90 time series of data, covering 31 years from 1962 to 1992 in the forested region north of Sapporo. What can ecologists decipher from a series of population estimates taken over a long period? Three types of analysis can be done: (1) amplitude and periodicity of fluctuations in density; (2) spatial synchrony among adjacent populations; and (3) presence and strength of density dependence and delayed density dependence. The patterns resulting from these analyses can be useful for generating hypotheses about the mechanisms behind the population changes, and feed directly into experimental analyses of these mechanisms. In practice, this gap has not been crossed, and the Hokkaido data are a rich source of pattern with no clear information about process.

Time-series analysis as it is currently practiced uses one data point per year, and for the Hokkaido data the fall density estimate has been used. This results in the unfortunate loss of the biological information captured in the spring and summer samples, which remain at present unanalyzed. The first observation on the 90 time series by Bjørnstad *et al.*⁴ was that the west coast populations of the grey-sided vole exhibited seasonal population fluctuations, while those in the more mountainous central regions showed three- to four-year cycles. West coast populations fluctuate less than inland populations, yet the standard deviations of the log abundances, s , form a continuous series averaging 0.4 and ranging from 0.3 to 0.5. The mechanisms behind this gradient from coastal to inland populations are not clear. Unfortunately, little is known of predator abundance or impact on voles in Hokkaido. There is a general gradient of more snowfall in the areas away from the coast, but whether direct climatic impacts affecting the length of the breeding season might be involved, or snow levels affect predation rates, is unclear.

A clearer picture might appear when further time-series are re-analyzed. Saitoh¹ hints at the riches waiting to be analyzed in his partial analysis of samples from the whole island of Hokkaido. To date, only the northwestern section of the island has been analyzed in detail^{2–4}. The Oslo group is

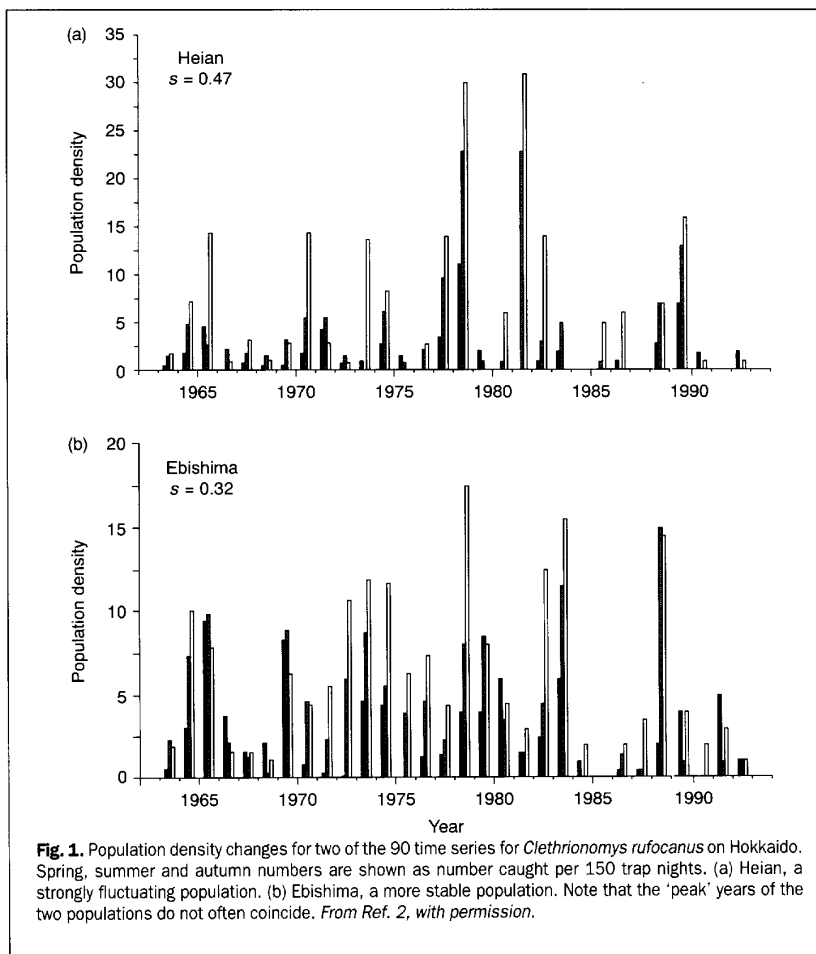


Fig. 1. Population density changes for two of the 90 time series for *Clethrionomys rufocanus* on Hokkaido. Spring, summer and autumn numbers are shown as number caught per 150 trap nights. (a) Heian, a strongly fluctuating population. (b) Ebishima, a more stable population. Note that the 'peak' years of the two populations do not often coincide. From Ref. 2, with permission.

actively pursuing the analysis of the entire data set and we can look for further advances.

There is a superficial similarity in the Hokkaido gradient with similar gradients in vole cycles in Fennoscandia⁵⁻⁷. Southern populations of voles in Fennoscandia tend to be more stable in numbers and northern populations more cyclic. The Fennoscandian gradient is associated with a gradient from generalist predators in the south to specialist predators in the north^{8,9}. Not every gradient of course must be explained by the same factors and one could postulate gradients in weather, vegetative productivity, or predation as possible explanations. The predation hypothesis is a good starting point for testing alternative views¹⁰, but detailed field tests are needed.

The time-series analysis of the 90 Hokkaido data sets by Stenseth and his associates sets a new standard for the application of time series to population data. A log-linear autoregressive model was fitted in four possible configurations:

$$\log\left(\frac{N_t}{N_{t+1}}\right) = a_0 + a_1 X_{t-1} + \dots + a_3 X_{t-3} + \varepsilon_t$$

where:

N_t and N_{t-1} = population size at time t and $t-1$

X_{t-1} , X_{t-2} = log of population size at time $t-1$ and $t-2$

ε_t = random noise.

This model has been previously used by Royama¹¹ and can describe a variety of population changes from those with no density dependence to those with time lags 1, 2 or 3. These models can describe both density-independent and direct density-dependent population dynamics, while lag 2 and 3 models add in possible delayed density dependence with two- or three-year time lags. The fit of the Hokkaido data is interesting – of the 90 time series the best fit was obtained with lags (d) for

$d = 0$ 41 series
 $d = 1$ 10 series
 $d = 2$ 33 series
 $d = 3$ 6 series

There is support here for any viewpoint (for instance, that population changes are often just random changes), but Stenseth takes a more sensible biological viewpoint that the most parsimonious model is $d = 2$, the time-lag model with one- and two-year time lags. We now have a quantitative way of measuring the strength of density-independence, direct density dependence (a_1), and delayed density dependence (a_2). The estimate of direct density dependence, a_1 , was effectively constant for all the popu-

lations, and statistically significant, indicating regulation of numbers. The delayed density-dependence coefficient, a_2 , varied among populations, with a trend toward lower values in the inland sites. Tests for density dependence by Saitoh³ have shown significant direct density dependence in virtually all of the 90 time series from Hokkaido, but only 10–15% of the series show delayed density dependence. Social inhibition of sexual maturation and generalist predators are the two mechanisms suggested by Saitoh for direct density dependence, while specialist predators are the preferred potential mechanism for delayed density dependence. These ideas await an experimental attack.

There are two important consequences of using the log-linear model given above. First, there is no nonlinearity in this model, and thus much of the interest in the features that arise from nonlinearity (like chaos) is absent. Second, this model is a phase-forgetting model¹², and thus produces damped oscillations rather than cycles. Certainly some of the populations on Hokkaido are cyclic¹, and this would appear to be a problem. But Royama¹¹ showed that linear models will give rise to limit cycles when you add environmental stochasticity, which is always present in the real world if not always in our models of it¹³.

The wealth of the Hokkaido vole data has provided an opportunity for small-rodent ecologists to merge together pattern studies via time-series analysis and process studies of mechanisms of population regulation. The classic work by Kalela¹⁴ on reproductive changes in the grey-sided vole in Finland, and work in Fennoscandia on movements and social organization of this species^{15,16}, along with Japanese work on the mechanisms behind these population changes^{17,18} have set the stage for more-detailed process studies.

All good things must end, and by the early 1990s the amount of new forests planted on Hokkaido was reduced, and vole damage is no longer severe. The Japanese Forest Agency has questioned whether there is any need to continue this extensive sampling program for vole density. But there is still much to be uncovered regarding spatial synchrony and seasonal dynamics in the time series not yet analyzed, and a rich set of possibilities now exist for experimental studies on predation and social dynamics to shed light on the patterns recognized. This Japanese–Norwegian collaboration has been, and will continue to be, most fruitful for understanding vole population dynamics.

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References

- Saitoh, T. (1987) A time series and geographical analysis of population dynamics of the red-backed vole in Hokkaido, Japan, *Oecologia* 73, 382–388
- Stenseth, N.C., Bjørnstad, O.N. and Saitoh, T. (1996) A gradient from stable to cyclic populations of *Clethrionomys rufocanus* in Hokkaido, Japan, *Proc. R. Soc. London Ser. B* 263, 1117–1126
- Saitoh, T., Stenseth, N.C. and Bjørnstad, O.N. (1997) Density dependence in fluctuating grey-sided vole populations, *J. Anim. Ecol.* 66, 14–24
- Bjørnstad, O.N. et al. (1996) Cyclicity and stability of grey-sided voles, *Clethrionomys rufocanus*, of Hokkaido: spectral and principal components analysis, *Philos. Trans. R. Soc. London Ser. B* 351, 867–875
- Bjørnstad, O.N., Falck, W. and Stenseth, N.C. (1995) A geographic gradient in small rodent density fluctuations: a statistical modelling approach, *Proc. R. Soc. London Ser. B* 262, 127–133
- Hansson, L. and Henttonen, H. (1985) Gradients in density variations of small rodents: the importance of latitude and snow cover, *Oecologia* 67, 394–402
- Henttonen, H., McGuire, A.D. and Hansson, L. (1985) Comparisons of amplitudes and frequencies (spectral analyses) of density variation in long-term data sets of *Clethrionomys* species, *Ann. Zool. Fenn.* 22, 221–227
- Hansson, L. and Henttonen, H. (1988) Rodent dynamics as community processes, *Trends Ecol. Evol.* 3, 195–200
- Hanski, I. and Korpimäki, E. (1995) Microtine rodent dynamics in northern Europe: parameterized models for the predator–prey interaction, *Ecology* 76, 840–850
- Korpimäki, E. and Krebs, C.J. (1996) Predation and population cycles of small mammals, *BioScience* 46, 754–764
- Royama, T. (1992) *Analytical Population Dynamics*, Chapman & Hall
- Nisbet, R.M. and Gurney, W.S.C. (1982) *Modelling Fluctuating Populations*, John Wiley & Sons
- May, R.M. (1973) *Stability and Complexity in Model Ecosystems*, Princeton University Press
- Kalela, O. (1957) Regulation of reproductive rate in subarctic populations of the vole, *Clethrionomys rufocanus* (Sund.), *Ann. Acad. Scienti. Fenn. Ser. A, IV Biologica* 34, 1–60
- Bondrup-Nielsen, S. and Karlsson, F. (1985) Movements and spatial patterns in populations of *Clethrionomys* species: a review, *Ann. Zool. Fenn.* 22, 385–392
- Imms, R.A. (1987) Responses in spatial organization and behaviour to manipulations of the food resource in the vole *Clethrionomys rufocanus*, *J. Anim. Ecol.* 56, 585–596
- Kawata, M. (1987) Pregnancy failure and suppression by female–female interaction in enclosed populations of the red-backed vole *Clethrionomys rufocanus bedfordiae*, *Behav. Ecol. Sociobiol.* 20, 89–97
- Saitoh, T. (1991) The effects and limits of territoriality on population regulation in grey red-backed voles, *Clethrionomys rufocanus bedfordiae*, *Res. Popul. Ecol.* 33, 367–386