



Rodent Fluctuations in Relation to Seasonality in Fennoscandia and Hokkaido

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Gradients and synchrony

For researchers studying population cycles in Fennoscandian small rodents, it is reassuring that a new gradient in fluctuation patterns has been detected in Hokkaido. Differences in fluctuation patterns have indeed been observed in many regions both in the northern and southern hemisphere; however, a distinct gradient has remained restricted to northern Europe until now. It is probably because there have been few other regions with such extensive studies of small rodents as in Fennoscandia and in Hokkaido.

In both regions the level of fluctuations, or 'cyclicality', has increased from temperate to boreal or subarctic conditions. The gradient covers a longer distance in Fennoscandia and reaches higher levels of fluctuations ('real cycles' over a larger region).

The gradients in Fennoscandia and Hokkaido provide a natural and interesting comparison, but it should be remembered that in spite of similarities, there are also a number of differences. Even if there is a gradient to more cyclic populations in north and east of Hokkaido, still only one third of the time series in the northeastern and central areas show significant multiannual cyclicality (Bjørnstad et al. 1998). This, combined with a different degree of geographic synchrony in comparison to northern Fennoscandia should be further considered in more detail than currently done. The geographic synchrony increases to northern and eastern Hokkaido and is at the level of 50 km. This is much less extensive than in northern Fennoscandia where available data suggest that the geo-

graphic synchrony may cover hundreds of kilometers (Henttonen et al. 1977; but see Steen et al. 1996). The degree of cyclicality and geographic synchrony seems to be intimately related, and may also suggest causes of fluctuations. The recent changes in vole dynamics in northernmost Fennoscandia also show the connection between cyclicality and geographic synchrony. With less pronounced fluctuations, the large scale geographic synchrony has clearly weakened.

With respect to regulating ultimate factors, even the most cyclic parts of Hokkaido cannot be compared with cyclic regions of northern Fennoscandia but rather with the transition zone in central Fennoscandia around 60°N, where both cyclic and noncyclic populations occur, and populations can turn from one stage to another. Hansson and Henttonen (1985) characterized the summer declines leading to very low fall densities during a cyclic crash as an essential part of true microtine cycles. They also suggested that these summer declines which occur synchronously in all sympatric vole species, are most probably caused by specialist mustelid predators. The occurrence of summer declines in the extensive Hokkaido data-sets and their geographic distribution in relation to some geographic patterns in predator community may give some insights about the role of predation. Henttonen et al. (1992) made a very preliminary estimate of summer declines in Hokkaido, and again the results corresponded to the Fennoscandian transition zone.

In this context, it would also be interesting to know the fluctuation patterns of other rodent species (and predators as foxes and other interacting species) in Hokkaido. No such analysis appears to have been performed in spite of evidence (Saitoh et al. 1998) of available data for *Apodemus* and other *Clethrionomys* species.³⁾ This should be done! We predict independent dynamics in the southwest but only limited synchrony in the north and east due to the fairly intermediate fluctuation patterns there.

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3) Editors notes: Data on *Apodemus* and other *Clethrionomys* species are available to northern populations. These data are indeed analyzed by Saitoh and Nakatsu (1997, *Mammal Study* 22: 27–38), Bjørnstad et al. (*Ecology* in press) and Saitoh et al. (*Ecology* in press). But their quality is not as good as the *C. rufocanus* data.

Possible dynamic effects of seasonality

The authors of this volume suggest more generally that the level of seasonality should in some way relate to the level of cyclicity. To scrutinize this proposition, it might be useful to examine to what extent northern Fennoscandia demonstrates greater seasonality than northeastern and northern Hokkaido.

First, Fennoscandia is covering more northern latitudes, particularly in areas with cyclic populations. In these northern areas there is little or no photoperiodicity either at mid summer or at mid winter. Such conditions may select for photoperiodically non-responsive morphs in northern Fennoscandia (Nelson 1987) but hardly so in Hokkaido. The fairly common winter reproduction (first of all *Microtus* and *Lemmus* spp.; for *C. rufocanus* winter breeding is generally very rare) in northern Fennoscandia may be related to such a selection. More generally, time of reproduction is very variable in northern Fennoscandian rodents but fairly constant in southern Scandinavia (Nyholm and Meurling 1979), except during mast seeding (Hansson 1984). These findings derive from several small rodent species. However, the conditions for *C. rufocanus* appear to be the opposite in Hokkaido where the breeding season is longer in the south than in the north (Saitoh et al. 1998).

The severity of the climate may be assumed to be stronger in northernmost Fennoscandia due to its latitude but this might actually not be the case; the Gulf Stream is ameliorating the climate of this region to a considerable extent. The duration of snow cover is, however, longer in northern Fennoscandia and mean summer temperature and, particularly, the growing season is longer in Hokkaido (Henttonen et al. 1992), although with fairly large variation also within Hokkaido (Stenseth et al. 1998). The longer summer in Hokkaido may cause negative effects on the food quality for the voles; plants will easily mature in Hokkaido while short summers and cool weather during the growing time will lead to nutritious plants with smaller content of hard-digestible cell walls and plant fibers in northern Fennoscandia (Langvatn and Albon 1986; Albon and Langvatn 1992; Sand et al. 1995). Also the concentrations of some secondary compounds in relation to nitrogen increase with temperature in *Vaccinium myrtillus*, the main food plant of *C. rufocanus* in Fennoscandia (Laine and Henttonen 1987). It is in this respect pertinent to remember the breeding pause in high density *Microtus agrestis* populations in mid summer (Myllymäki 1977), paralleling a similar pause in *C. rufocanus* in southern Hokkaido (Saitoh et al. 1998).

The longer winters in northern Fennoscandia may imply better or prolonged protection against predators that are active above the snow in winter. Hokkaido has a large

number of generalist or only summer-active predators (snakes; Henttonen et al. 1992) that may reduce vole densities during summer. The occurrence of snakes as a dominant part of the predator fauna is particularly interesting as these species may show abundances and predatory activities that are negatively related to the climatic gradient but positively related to the population stability of the Hokkaido voles. There are few or no snakes in northern Fennoscandia but they are not very important in southern Scandinavia either. Snakes may preferably attack nests and nestling and have a qualitatively different influence compared to the mammals and birds that constitute almost the entire Fennoscandian predator fauna. It would be very interesting to know more about the predation and its geographic patterns in Hokkaido. As shown by Korpimäki and Norrdahl (1989), a rich community of avian predators can greatly reduce the numbers of least weasels, which may have dynamical consequences. A geographic analysis on the distribution of communities of snakes and avian predators could give hints for further detailed studies.

In spite of many interesting articles in this *Special Feature*, the strong emphasis on only social factors regarding the population dynamics of *C. rufocanus* in Hokkaido may not be warranted. Detailed demographic studies help us to focus on relevant mechanisms in the population regulation, but demographic studies alone do not solve the problem of untangling the causes of different kinds of fluctuations. In an experimental approach, knowing demography in detail helps to understand the mechanisms. Thus, there appear a number of other factors than social behavior that potentially may govern the Hokkaido gradient. The stronger density-dependence in winter than in summer in Hokkaido appears difficult to understand and the authors are evidently looking for crucial social systems hitherto unknown due to limited winter studies. This search for new social processes is indeed commonplace in cycle research but has not been very successful.

It should, however, be considered that the stronger winter density-dependence could be a consequence rather than a cause of the fluctuation patterns. Such density-dependence may only appear temporarily at high winter densities, or perhaps at high densities in relation to food resources. Other factors may determine the rate of population growth over summer and the resulting fall peak numbers while limiting winter food, or attraction of specialist predators or parasites, may cause severe density-dependent (or lagged density-dependent) effects only during population peaks. Such competition or predation might be more pronounced or efficient the longer the winter is.

For an alternative, or rather complementary, explanation we first raise a technical question about measuring differences in seasonal density-dependencies. Spring sam-

pling in Hokkaido was done in May/June, which is about two months after snow melt. Also the breeding season of gray-sided voles starts in March/April. Therefore, the most intensive social interactions, those when voles mature and establish breeding territories or home ranges, take place at least a month or two before the 'spring' sampling. Intuitively, social interactions connected with 'summer' breeding, should be included in summer season, and the winter should basically reflect density-dependence in the nonbreeding season. Now it may well be that the results of higher density-dependence in winter only reflect social interactions at the beginning of the breeding season, and in that sense has actually nothing to do with winter itself, like resource limitation, protective snow cover etc. If the spring trappings had been done immediately after snow melt in late March/early April (a mere technical difference), most social interactions connected with establishment of breeding territories might have taken place in the period now defined as summer. We suggest that, if possible, seasonal density-dependencies should be analyzed in relation to the biological processes being studied.⁴⁾

How to keep momentum

Thus, several options still remain to explain the two gradients. For researchers using observational data two approaches prevail: To refine the analyses of present gradients or to find new gradients. With the effort allocated to the Hokkaido gradient and the relative paucity of data within the extensive Fennoscandian gradient, only the second alternative appears viable after the publication of this extensive Hokkaido volume. New gradients should be short to provide superior cost-benefit, although in short gradients movements of predators may confound the patterns. They should also, if possible, include gradients in fluctuations in other taxa than small rodents in order to possibly establish still more general patterns. Such a spatially limited gradient that comes to mind is that of the larch budworm in the European Alps (e.g. Baltensweiler 1993), with differences in fluctuation patterns within kilometers or less. Recently there have been started a lot of studies of small rodents in this region, even by the authors of the present volume, and analyses of fluctuation patterns from, say, downtown Lyon with intervals of a few km to the summit of Mont Blanc may be rewarding. This is a far cry compared to what is expected from rodent ecologists in general by Yoccoz et al. (1998).

4) Editors notes: Notice that the model developed and discussed by Stenseth et al. (1998) refers to the length of the proper breeding season, just as asked for by Hansson and Henttonen. Their point of the fall-to-spring period between the spring samples and the fall samples also includes the beginning of the summer breeding period; this will certainly be an empirical problem in future analyses of the seasonal data.

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