

Rodent dynamics and community structure: *Clethrionomys rufocanus* in northern Fennoscandia and Hokkaido

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The grey-sided vole *Clethrionomys rufocanus* shows more pronounced fluctuations (cycles) in northern Fennoscandia than in Hokkaido. The interacting fauna of Hokkaido is palearctic and the climate temperate while in northern Fennoscandia the fauna is palearctic and the climate boreal-subarctic. The predator-prey community in northern Fennoscandia is dominated by resident specialist predators with few species of alternative prey, whereas a multitude of alternative prey for numerous generalist predators exists in Hokkaido. This suggests population regulation by generalist predators in Hokkaido in accordance with recent conceptual and mathematical models. The more diverse community and more stable vole dynamics in Hokkaido appear to be related to shorter duration of snow cover but not to the maximum snow depth.

1. Introduction

Population dynamics of rodents show strong geographic variation, and the composition of animal communities may account for these differences in population fluctuations (Hansson & Henttonen 1985a, 1988, Hanski et al. 1991). The need for some explanation has been brought into focus by two recent analyses of fluctuation patterns of a palearctic rodent species, *Clethrionomys*

rufocanus in northern Fennoscandia (Hansson & Henttonen 1985b) and in Hokkaido (Saitoh 1987), with very different outcomes. This species was strongly cyclic in northern Fennoscandia but almost noncyclic, with minor peak years at best, in Hokkaido.

Differences in the physical environments or in the biotic communities of northern Fennoscandia and Hokkaido could cause these differences in dynamics. Still, physical and biotic

conditions seem fairly similar in the two regions; both faunas are strictly palearctic. Here we attempt an unorthodox and qualitative analysis of environmental variables to establish which factors may be most important for the different regional dynamics. Thus, we make qualitative comparisons of extrinsic factors for two remote areas, and we try to deduce the dynamic effects of differences in physical and biotic environments.

2. Methods

Comparisons of amplitudes of fluctuations are based on density estimates and cyclicity indices (Hansson & Henttonen 1985a). These indices also reflect periodicity, as only multiannual fluctuations in *Clethrionomys* spp. have resulted

in high values of these indices (Henttonen et al. 1985). To understand the differences in fluctuations we compare such factors that have been implicated to influence rodent dynamics, i.e. climate, habitat characteristics and interacting community agents. We do not have any global information on important diseases or parasites of *C. rufocanus*, so we restrict our community analysis to food, competition and predation. Alternative prey species for generalist predators are also examined as such species may be important in stabilizing rodent dynamics (Loman 1988). We provide references when applicable and adequate; but some of the information is due to our personal experience. The Hokkaido data apply for the whole island while the Scandinavian data come from Pallasjärvi, Kilpisjärvi and the adjoining Finnish-Swedish border areas (67–69°N,

Table 1. Climate and habitats surrounding *C. rufocanus* in northern Fennoscandia and Hokkaido.

	Fennoscandia	Hokkaido
Snow duration, months	7–8	4
Mean maximum snow depth, cm	70–100	50–250
Mean July temperature, °C	13–15	11–24
Growing season, days > 5°C	95	197–234
Habitats		
Optimum	Northern coniferous and subalpine birch forests with <i>Vaccinium myrtillus</i>	Mixed forests and broad leaved forests with <i>Sasa</i> spp. bamboos
Suboptimum	Mountain tundra and bogs in boreal zone	Coniferous forests

References: Kalela 1957, Viitala 1977,1987, Henttonen et al. 1977, SDMO 1982, Masuda 1983, Ota 1984, Järvinen 1987, SMHI 1988.

Table 2. Food of *C. rufocanus* in northern Fennoscandia and Hokkaido.

	Fennoscandia	Hokkaido
Staple food		
Summer	Various forbs and <i>V. myrtillus</i> (young shoots)	Various forbs and <i>Sasa</i> bamboo (young shoots)
Winter	<i>V. myrtillus</i> (young shoots)	<i>Sasa</i> bamboo (shoots, buds and leaves)
Auxillary food		
Summer	Various dicot. species	Various dicot. species
Winter	Bark	Bark

References: Kalela 1957, Hansson & Larsson 1978, Suga 1980, Ota 1984.

20–25°E), where long-term data on *Clethrionomys rufocanus* are available.

3. Results

3.1. Fluctuation patterns of voles

Analyses of long-term population studies from extensive areas in northern Fennoscandia ($n = 3$) demonstrated cyclicality indices between 0.67 and 0.87 (Hansson & Henttonen 1985b and consecutive observations), while those from Hokkaido ($n = 7$) only ranged between 0.24 and 0.42 (Hansson & Henttonen 1985b, Saitoh 1987). The difference between the two regions, including all published data was clearly significant (Mann-Whitney $U = 0$, $P < 0.01$) and on-going studies in northern Fennoscandia (Henttonen et al., unpubl.) indicate further cyclicality indices there well above 0.5.

There were two further differences between northern Fennoscandia and Hokkaido. Even in low years some 5 animals were caught per 150 trap nights in Hokkaido (Fig. 3 in Saitoh 1987) while the corresponding figures for Fennoscandia have been in the order of 0.1 animals per 100 trap nights (Hansson and Henttonen 1985a). There were also areas in Hokkaido with very small and irregular density variations between years (Type A in Saitoh 1987) while this type of density variation is not known for *C. rufocanus* in northern Fennoscandia.

3.2. Physical environment

Although snow cover can be very deep both in northern Fennoscandia and in Hokkaido (Table 1), there is a pronounced difference in the length of the snowy season, being almost double in northern Fennoscandia. This is reflected in the length of the growing season, here defined as days with a mean temperature above 5°C, which is more than twice as long in Hokkaido as in northern Fennoscandia. Mean summer temperatures for the two regions overlap, though Hokkaido can be much warmer. Habitat choice of *C. rufocanus* is very generalized in both regions, and the species occurs in almost all habitats

and only shows weak preferences. However, it generally is most abundant in southern types of forests (and managed fields) in Hokkaido and from boreal forests high up above the timberline in northern Fennoscandia.

3.3. Food habits

The main food component differs conspicuously between northern Fennoscandia and Hokkaido (Table 2), being the dwarf shrub *Vaccinium myrtillus* and bamboo grass *Sasa* spp, respectively. Both items are very common in the environments of *C. rufocanus*, as are the other food types taken in either summer or winter. Thus food habits of this species seem as generalized as habitat choice, and *C. rufocanus* can be characterized mainly as a folivore, with an unusually wide diet breadth for a *Clethrionomys* species (Hansson 1985).

3.4. Interspecific competitors

Other *Clethrionomys* species are generally subordinate to *C. rufocanus* (Table 3). Thus, although they often share habitat, they do not seem to affect the dynamics of our target species. In Fennoscandia, *Lemmus* and *Microtus* species are superior competitors but do not overlap extensively except during peak years (Viitala 1977, Henttonen et al. 1977, Henttonen & Hansson 1984). There are no *Microtus* or *Lemmus* species

Table 3. Common syntopic microtine species which could be interspecific competitors for *C. rufocanus* in northern Fennoscandia and Hokkaido.

	Fennoscandia	Hokkaido
Dominant		
<i>Lemmus lemmus</i>	+	
<i>Microtus oeconomus</i>	+	
<i>Microtus agrestis</i>	+	
Subordinate		
<i>Clethrionomys glareolus</i>	+	
<i>Clethrionomys rutilus</i>	+	+

References: Henttonen et al. 1977, Henttonen & Hansson 1984, Ota 1984, Viitala 1984.

in Hokkaido. Thus, interspecific competition seems unlikely to affect population increases of *C. rufocanus* either in northern Fennoscandia or in Hokkaido. However, predation rates may be influenced by syntopic species (Loman 1988).

3.5. Predators and alternative prey

There are few predator species in northernmost Fennoscandia (Table 4), and this applies especially to generalists. Specialists and nomadic predators may be fewer in Hokkaido while the generalists are more numerous there. At the same time the number of alternative prey species, and their abundance, is much higher in Hokkaido. Generally, the fauna of both predators and alternative prey is a much more southern one in Hokkaido than in northern Fennoscandia. Thus, the predators *Asio otus*, *Mustela vison*, *Nyctereutes procyonoides*, *Strix uralensis*, *Buteo buteo* and *Circus aeruginosus* occur also in central or southern Fennoscandia, but south of the distribution range of *C. rufocanus* (*M. vison* has spread only recently into the northernmost Fennoscandia). In this southern Fennoscandian region they co-occur and partly prey on *Tetrastes bonasia*, *Sciurus vulgaris*, *Apodemus* and *Rana* (e.g. *R. temporaria*) species. Similarly, snakes, though different species from those in Hokkaido, are important predators only in southernmost Fennoscandia.

4. Discussion

Our analysis shows clearly that the functional communities surrounding *C. rufocanus* are very different in northern Fennoscandia and in Hokkaido. In the former area there are few alternative prey species and, as a consequence, few generalist predators while a much richer community has developed in Hokkaido. One reason for this difference is obviously that snow covers the ground for considerably more than half a year in northern Fennoscandia but much less in Hokkaido, permitting the existence of more species from the temperate region in the latter area. When analyzing the Fennoscandian north-south gradient in microtine cyclicity Hansson & Henttonen (1985a) could not separate the effects of snow depth and duration because they both were

strongly correlated with latitude. In the present comparison, however, the length of the snowy period seems much more likely to be important than the maximum amount of snow.

The shorter snow duration, and consequential a diversified predator and prey community in Hokkaido, predicts dampened fluctuation patterns according to a theoretical model developed by Loman (1988). Switching between *C. rufocanus*

Table 4. Predators and alternative prey for the predators in northern Fennoscandia and Hokkaido.

	Fennoscandia	Hokkaido
Predators		
Specialists		
<i>Mustela erminea</i>	+	+
<i>M. nivalis</i>	+	+
Nomadic		
<i>Stercorarius longicaudus</i>	+	
<i>Buteo lagopus</i>	+	
<i>Surnia ulula</i>	+	
<i>Asio otus</i>		+
Generalists		
<i>Vulpes vulpes</i>	+	+
<i>Alopex lagopus</i> (rare)	+	
<i>Mustela itatsi</i>		+
<i>M. vison</i>		+
<i>Martes zibellina</i>		+
<i>Nyctereutes procyonoides</i>		+
<i>Strix uralensis</i>		+
<i>Buteo buteo</i>		+
<i>Circus aeruginosus</i>		+
<i>Elaphe climacophora</i>		+
<i>E. quadrivirgata</i>		+
<i>E. conspicillata</i>		+
Alternative prey at rodent lows		
<i>Lepus timidus</i> (ind./ha)	0.02–0.03	0.06–0.08
<i>Lagopus lagopus</i> (ind./ha)	c. 0.02	
<i>Tamias sibiricus</i> (ind./ha)		0.1–0.6
<i>Tetrastes bonasia</i>		+
<i>Sciurus vulgaris</i>		+
<i>Apodemus argenteus</i>		+
<i>A. speciosus</i>		+
<i>Rana temporaria</i>		+

References: Matsuoka 1974,1977, Andersson 1976, Misawa 1979, Yoneda 1979,1982, Yoneda et al. 1979, Oksanen and Oksanen 1981, Ota 1984, Shibata 1985, Henttonen et al. 1987, Uruguchi et al.1987, Oksanen 1990, Hanski et al. 1991.

and alternative prey will be much easier for generalist predators in Hokkaido than in northern Fennoscandia, as it is easy for generalists to switch between *Microtus agrestis* and alternative prey in southern Fennoscandia (Erlinge 1987, Erlinge et al. 1983). Thus, we find the different fluctuation patterns in the two regions to agree with the suggestions by Hansson & Henttonen (1985a) that rodent cyclicality varies positively with amounts of snow and that simplified communities will generally show fluctuations of high amplitudes.

This hypothesis was developed from Fennoscandian data, and we consider the pattern found in Hokkaido as an independent test for the idea, not merely as one additional degree of freedom into our earlier data. It seems that microtine dynamics are related to snow in regions with maritime snow. However, we wish to emphasize an important point regarding snow cover. Hansson & Henttonen (1985a) showed that there was no correlation between microtine dynamics and snow cover in North America. As we pointed out, this could be due to the quality of snow. The powder-like continental snow in north-boreal America clearly differs from the dense maritime snow in Fennoscandia and Hokkaido. One other factor may stabilize the dynamics in Hokkaido: North Fennoscandian cycles reach their high amplitude because of continuing rodent declines during summer, resulting in very low autumn densities during most crash years. However, if in regions such as Hokkaido, there are some additional alternative prey available during summer, the predators might then switch to such prey instead of continuing predation on the depressed microtine populations (Hansson & Henttonen 1985a).

There was at least one such prey item in Hokkaido, viz. the hibernating Siberian chipmunk *Tamias sibiricus*, which may attain rather high densities. By contrast, there is a complete lack of hibernating sciurids or other hibernators in northern Fennoscandia. Amphibians and migrating birds are other possible summer prey, but less similar to *Clethrionomys* than are the chipmunks. It should also be pointed out that *T. sibiricus* occurs as close to Fennoscandia as in the Archangelsk region of the USSR, where there are no pronounced cycles in *Clethrionomys* (Hansson & Henttonen 1985b).

It is not wholly clear why *C. rufocanus* occurs in a temperate-boreal climate in Hokkaido but not in Fennoscandia. The occurrence of the ubiquitous *C. glareolus* in Fennoscandia but not in Hokkaido may cause problems to *C. rufocanus* due to scramble competition. On the other hand, there is also some evidence that unimportant parasites of *C. glareolus* may be fatal to *C. rufocanus* introduced south of its normal distribution (Viitala et al. 1986). The abundance of *C. rufocanus* in Hokkaido may also be due the absence of all *Microtus* species. On Honshu *M. montebelli* is common and *C. rufocanus* absent.

Finally, *C. rufocanus* occurs over vast areas between Fennoscandia and Hokkaido. An 18-year study of this species on clearcuttings in northern China (Xia et al. 1985) showed a cyclicality index of 1.58, which is intermediate between the patterns in Hokkaido and in northern Fennoscandia, but nothing was mentioned about the composition of the surrounding community. No other long-term information has been available on central Eurasian *C. rufocanus* populations. From our present and earlier findings, we predict that patterns of dynamics in future (or rediscovered) studies on *C. rufocanus* will be related to the interacting communities, with fairly stable populations in temperate and continental boreal areas but cyclic ones in maritime boreal-subarctic areas with long duration of snow cover and less diverse predator-prey communities.

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