



Whither Small Rodent Population Studies?

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Small rodents have been for many years model organisms for studies of population dynamics for three reasons. First, they are conveniently short-lived so that a post-graduate student can accomplish something within the constraints of a 3–4 year time window. Second, they are ubiquitous, occur in abundance nearly everywhere, and are occasionally of economic importance (Singleton 1997; Stenseth and Saitoh 1998). Third, they do interesting things such as have population cycles. All these features have combined to produce a very large literature on rodent populations that is somewhat overwhelming to the novice. It is important therefore to step back and ask what we have accomplished and what is to be done next. This series of papers on *Clethrionomys rufocanus* provides an ideal time to address these larger issues, both for this particular species and for other small rodents.

I address here three points – the optimal population dynamics data-set, the shortcomings of the current data on *C. rufocanus*, and the problems and opportunities of the future.

Optimal population data

It is useful to start by asking what an ideal world of population data would look like. It would have four components.

1. **Time scale.** We would like to have data covering at least 10 of the population events shown by the species. If we are studying a 3–4 year cycle in northeastern Hokkaido, we would like 30–40 years of data. In the present studies we have time series up to 31 years long, admirably close to this goal. If we are studying annual dynamics, such as *Apodemus* in Hokkaido, we would be happier with shorter time series.
2. **Spatial scale.** We would like data from many populations spread over the geographic range of the species. The spatial resolution of these data would depend on the covariation among sites in a given neighborhood. There are so little data of this type

available for small rodents that it is a necessary part of future work to obtain such data. But the Hokkaido data are exceptional (Saitoh et al. 1998) and this *Special Feature* illustrates the spatial component of population dynamics in detail, and begs us to get more data of this type on other small mammals.

3. **Individual scale.** We need to understand the mechanisms behind population changes, and we can obtain this understanding only by having detailed data on individuals. For *C. rufocanus* we do not have enough data at this scale (Yoccoz et al. 1998). The critical data needed on individuals depend on the mechanisms proposed to explain the dynamics. If you are concerned about the role of mustelid predators in causing population changes, you must determine the fraction of individuals killed by these predators. If you think infanticide causes a reduction in early juvenile survival, you must obtain data on the frequency of infanticidal intrusions (Wolff and Cicirello 1989).
4. **Community scale.** We can treat all small mammal studies as single population studies but it may be more fruitful to consider interactions between species in the community as potential influences on dynamics. We typically think only of predators but parasites and diseases should be considered as well (Saitoh and Takahashi 1998), as well as competitors for food resources. In Hokkaido competition for resources between species is presumed to be minimal, and these community interactions can be ignored. Generalist predators are perhaps the most common factor operating on small mammals in which community interactions, including indirect effects (Menge 1997), need to be considered.

Shortcomings of the *Clethrionomys rufocanus* data

Given this ideal world, it is relatively easy to pinpoint the shortcomings of the Hokkaido data. While these data score an Olympic-style (with a top score of 6.0) 5.8 on

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temporal and 5.9 on spatial scale, at the individual scale it reaches only 4.5 and at the community scale only 2.0. These ratings should be seen against a background, as pointed out by Stenseth and Saitoh (1998), that *C. rufocanus* is far ahead of all other mammal and bird species on both temporal and spatial scales. Only the Fennoscandian rodent data come close, and by contrast there is nothing in North America that would rank at all on these temporal and spatial components for small rodents.

In spite of these deficiencies, there is no shortage of hypotheses to explain the density-dependent and the delayed density-dependent components of the time series models for *C. rufocanus* (Bjørnstad et al. 1998). Early work by Fujimaki (1975) on reproduction and later work by Kawata (1987) and Saitoh (1991) are just a few examples of the details of the demographic machinery that are useful for generating hypotheses about the factors causing population density changes. The review of social processes in *C. rufocanus* by Ishibashi et al. (1998a) highlights the need to determine kinship effect on reproduction and juvenile survival. Specific hypotheses need to be tested in field populations and this is a critical next step for *C. rufocanus*. I think at this stage it would be most useful to articulate specific hypotheses and alternative hypotheses to explain the dynamics of this species in the cyclic zone and in the zones of irregular fluctuations. Stenseth et al. (1998) interpret the gradients on Hokkaido as a result of differing lengths of summer and winter, coupled with different density-dependent relationships within each season. This hypothesis deserves a closer look. We need to know the mechanisms behind the density-dependent relationships, and in particular we need to know if the winter losses are gradual or rapid. For example, if spring declines (Krebs and Boonstra 1978) were a significant part of winter losses, the food-based or predator-based explanations for differences in winter survival might be less important. The important point is to do some experiments to investigate the origin of seasonal differences.

Problems for future work

I address here three problems that I think are central to future studies on Hokkaido *Clethrionomys rufocanus*.

Should further monitoring be initiated? I would strongly recommend that monitoring be started again on at least a minimal set of sites in the cyclic zone and in the southern areas where cycles are not present. I think two areas in each would be minimal, and these could be used as controls for population experiments. In view of the uncertainty of climate change impacts, this monitoring could be justified solely as a biological equivalent of the Mauna Loa

CO₂ data (see Keeling 1986).

What experimental work should have priority? This is a difficult question because we all have strong biases. I would recommend a predator removal experiment like that of Korpimäki and Norrdahl (1998) coupled with a detailed study of demography as suggested by Yoccoz et al. (1998) so that demographic change can be related directly to predator offtake. I would also recommend further studies on the role of social behavior in regulating reproduction in field populations with the focus on how large these effects are in the overall population changes of *C. rufocanus* (as recommended by Ishibashi et al. 1998a). Lambin and Yoccoz (1998) have led the way in this type of experiment.

What gaps remain in Clethrionomys rufocanus ecology? We know very little about many other aspects of the ecology of this rodent, and it is not clear what further knowledge might be useful in the future. For example, information on the population genetic structure of *C. rufocanus* is lacking. We do not know the relationship between local population synchrony in numerical dynamics and local population genetic structure (e.g. Stacy et al. 1997). We need much more detailed data on reproductive rates and survival rates from mark-recapture studies. What demographic impact, for example, do the winter kin groups have (Ishibashi et al. 1998b)? Is dispersal between local populations common or rare?

In part some of these kinds of studies will be shooting-in-the-dark, but we should consider whether or not to treat *C. rufocanus* as the *Drosophila* of small mammal research for the millenium.

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