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The Konnevesi symposium on *Clethrionomys* biology

Conclusions: A speculative account

Now that we know approximately where we are, it seems natural to ask where future research should be concentrated. It is fair to conclude that several populations of some *Clethrionomys* species (e.g., *C. glareolus* and *C. rutilus*) are fairly stable (or at least not multi-annually cyclic) whereas several other populations of the same species are multi-annually cyclic with respect to density. Furthermore, one species (i.e., *C. rufocanus*) seems to be cyclic throughout its range (possibly with the exception of Japan), whereas another species (i.e., *C. gapperi*) seems to be non-cyclic throughout its range. Unfortunately we do not understand why this is so. Specifically why is, for example, *C. rutilus* cyclic in northern Scandinavia and non-cyclic in Alaska?

It is further fair to tentatively conclude that the four thoroughly studied species, *C. gapperi, C. glareolus, C. rufocanus* and *C. rutilus*, all seem to exhibit the same social system of female territoriality. This means that a female must have a territory in order to breed. Unless territory size varies with density (which it does not seem to do), this feature of *Clethrionomys* may be — and probably is — a strong stabilizing factor. However, our current understanding of this system of territoriality is based on studies of fairly stable and non-cyclic populations. It would be nice if a study comparable to the one reported by Bujalska (pp. 331–342) was carried out on a properly cyclic population.

If territory size changes, however, instability of population density may result if, for example, the habitat quality changes in response to the density increase. This change in habitat quality could result from plant-herbivore interaction. Whether such cycles would at all be like those actually seen in cyclic *Clethrionomys* populations is, of course, an open question. Much more empirical and theoretical work is required before we can provide an answer.

Both cyclic and non-cyclic populations of *Clethrionomys* seem rather uniform with respect to social organization. This makes this group of species very suitable for studying "why cycles"? By their uniformity, the variability in comparative studies is greatly reduced. It seems (to me, at least) that differences in the environmental setting in which various populations are living may be of great importance in determining the population dynamic patterns.

We know more: in some of the regions where we find the really cyclic populations, winter is the longest season of the year. Some work has been done on the winter ecology of *Clethrionomys* (e.g., Fuller, pp. 243–255; Ylönen & Viitala, pp. 353–358). For example, we know that the social structure of a given population changes with the seasons; but, as far as I understand, we have not the slightest idea what population dynamic consequences this has. Certainly, studying the seasonal changes in social structure and the population dynamic consequences is of paramount importance for a better understanding of *Clethrionomys* biology — and, in fact, of microtine biology in general. Again, both stable and cyclic populations should be studied in a comparative manner. Since this has not been the approach adopted, I am *not* convinced that Fuller's (pp. 229–241) somewhat pessimistic view on the outcome of studies on winter ecology is justified.

Where should we go from here? I guess we all wish we could provide well justified recommendations; anyway, here I list some of the recommendations which emerged during discussions at the Konnevesi meeting:

1) Carry out correlative studies along the lines described by Hansson (pp. 319–328) and Hansson & Henttonen (pp. 277–288) on both stable and cyclic populations. Preferably, such studies should be done both in a north-south and in a east-west gradient; the distribution of cyclic and stable populations within the same *Clethrionomys* species certainly allows us to do so (see pp. 298, 331–351). In my mind, the

studies on Crab Apple Island (Bujalska, pp. 331–342) are an ideal model for such a comparative study: the same kind of intensive study should be carried out on a cyclic population. In such studies it would be important to examine whether some populations always are maintained at densities below the limit set by territory size, and whether other populations frequently expand beyond such a limit. In particular, it would be important to find out whether this has something to do with cyclicity or not.

2) We need a better understanding of how reproduction and survival are influenced by social and ecological factors. The studies reported by Gustafsson (pp. 303–308) and Gustafsson & Batzli (pp. 273–276) serve as good examples here. Even though we know much about the ecological aspects associated with the spacing behaviour of *Clethrionomys* (e.g., Bujalska, pp. 331–342; Gipps, pp. 343–351; Bondrup-Nielsen, pp. 373–383; and Bondrup-Nielsen & Karlsson, pp. 385–392), we are just beginning to understand the underlying physiological and behavioural mechanisms (but see Gustafsson, pp. 303–308; and Viitala & Hoffmeyer, pp. 359–371). In particular, we should pay more attention to the individual animal — and in particular to how dispersing individuals affect resident animals and vice versa (Gustafsson, pp. 303–308; discusses some relevant experimental approaches). Finally we should try to understand why, in extensively cyclic populations, so many individuals die, presumably *in situ*. Such a study is difficult to perform (e.g., how often do we see dying individuals?), but it is certainly important.

3) In our studies on population biology of *Clethrionomys*, we have somehow forgotten the environment: hence, in studies on *Clethrionomys* we should probably pay more attention to the biotic environment (e.g., predators and food) and above all to the dynamic interactions between *Clethrionomys* and their biotic environment. And, of course, we should not forget the abiotic environment: for example, what effects does seasonality have on the biological performances of the animal? What effects do unpredictable events in harsh environment have? It would, furthermore, be worth while to try to understand what determines spring density: is it primarily density-independent (abiotic) effects, or is it density-dependent effects (with respect to winter density and/or the previous fall density; see Fuller, pp. 243–255)?

4) One aspect of the environment needs particular attention: even though "habitat heterogeneity" and "patchiness" (etc.) are popular terms nowadays, we do not really understand what a patch is. Carefully designed experiments are needed so that the animals somehow can "tell" us what defines a patch — and what distinguishes a good patch from a bad patch (see, e.g., Bondrup-Nielsen, pp. 373–383). We need an equally good understanding of the spatial dynamics of *Clethrionomys* populations as we have of their temporal dynamics.

5) Too little attention has been paid to monitoring, and understanding, possible changes in age structure of both stable and cyclic populations. Age structure introduces, of course, time lag effects into the population dynamics: hence, studies on the age structure of populations with different dynamics might provide cues for why some populations are stable whereas other are cyclic.

6) We ought furthermore to tie theory and data more closely together: theories ought to be made biologically more plausible and predictions have to be deduced with specific populations in mind. Above all, vague — handwaving — arguments so common in ecology should be avoided. It is only by asking Nature precise questions that we can hope to obtain interpretable answers: we should never forget that data, always, are gathered with reference to some view — hence, it is important to have as clear ideas as possible about what these views are.

7) Finally, we ought to do experiments in both the laboratory and in the field. Even more, we ought to — as pointed out repeatedly above — do experiments of a comparative type on stable and cyclic populations. Such experimental work ought to be designed so as to assist the interpretation of the results emerging from the kind of correlative studies recommended in item 1) above.

Studies along such lines are important for several reasons. They are important in order to obtain a better understanding of *Clethrionomys* biology in general, and *Clethrionomys* population ecology in particular. Studies on *Clethrionomys* biology are also important for the progress in the study of population regulation and for general population theory, since natural experiments are "performed"

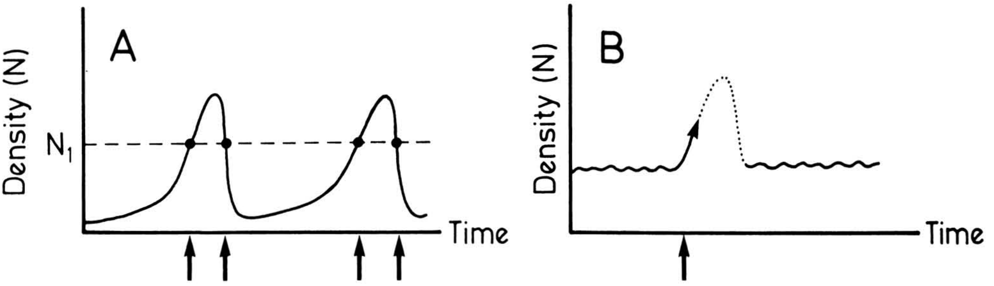

Fig. 1. Dichotomy between a fairly regularly cyclic population (A), and a mainly stable low density population which at irregular intervals "explodes" (B). Arrows along the time-axis indicate when it might be most important to investigate the populations in order to understand what generates these patterns; obviously studies at other times are important too — but the arrows indicate phases from which critical insights, needed for understanding the particular dynamics, might be obtained. N_1 represents an arbitrary density value so that, during a short time interval, the population density is equal to N_1 but in one phase in an increasing population and at a later phase in a decreasing population; see text for discussion.

regularly in these cyclic species. Among the small rodents, *Clethrionomys* is — because of its presumed homogeneity — an excellent group to work with.

Let me conclude this account by bringing up an intriguing issue worth thinking about.

Even though I cannot defend this point of view very strongly, I feel there might be a dichotomy in the population dynamics of *Clethrionomys* populations which has not previously been paid sufficient attention to (Fig. 1):

i) The typical cyclic *Clethrionomys* dynamics are caricatured in Fig. 1A: here the most important questions might be what causes the population crash, and what characteristics (demography, behaviour, etc.) distinguish an increasing population of a certain density (N_1, say) from a decreasing population of the same density?

ii) Non-cyclic, but fluctuating, populations of *Clethrionomys* may exhibit a population dynamic pattern as caricatured in Fig. 1B: the most important questions might be what causes the population to "explode" from time to time and whether there in fact exists a locally stable (in a mathematical sense) low, non-resilient (to use Holling's concept) equilibrium.

Certainly, we would study such populations (if the dichotomy is real) differently since we are interested in answering different questions in the two cases. The former question (Fig. 1A) is what I believe students of cyclic microtines have in mind. However, to have such a view on the biological system if in fact the population is behaving more as in Fig. 1B, would certainly be rather inappropriate. In the former case, one would concentrate more on the crash phase (Fig. 1A) whereas in the latter case one would concentrate more on the early increase phase (Fig. 1B).

Above all, we need a multitude of approaches — both empirical and theoretical. As editor of this special issue of Ann. Zool. Fennici, I hope that the various approaches — and ways of looking at the problems — exemplified in these papers and brought up in the concluding commentary may help us remember some of the more rewarding ways of approaching the question "why are some populations cyclic and other populations stable?"

Acknowledgements. The above is a summary account of a round-table discussion, held on the last day of the Konnevesi-meeting: this summary would have been impossible without the participants and their willingness to share ideas and data. I thank them all. Part of the round-table discussion was a psychological experiment where the participants were asked to write down — rather uncritically — what first came to their mind when I asked "What is the most important question in *Clethrionomys* biology?" Subsequently these views were discussed in a rather critical way: by so doing, we hoped to separate the *creative* (but not necessarily critical) phase of science from the *critical* phase of science. The above summary is based on this experiment, but it is of course my own interpretation of what was said during this round-table discussion: I certainly take the responsibility for any shortcomings in the above summary and for any misinterpretations.

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