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Commentary

Female relatedness and microtine population dynamics: experience from cyclic populations

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Charnov & Finerty's (1980) hypothesis of the impact of relatedness between individuals on the multiannual fluctuations of microtine populations (cyclicality) has initiated a number of field experiments in the Holarctic region (Kawata 1987; Boonstra & Hogg 1988, Ylönen et al. 1990).

During recent years, the Charnov-Finerty hypothesis has been shown to be insufficient in explaining population cycles (e.g. Kawata 1990, Pugh & Tamarin 1990, Stenseth & Lomnicki 1990). Lambin & Krebs (1991) presented a new general model for all microtines of the impact of relatedness on the population fluctuations. In the present paper we go through some of the assumptions of the Lambin-Krebs model about the formation of social spring groups, occurrence of spring declines and their possible impact on the following summer's demography. The paper is based on our long-term data on social organization and demography of the bank vole *Clethrionomys glareolus* but studies on other *Clethrionomys* species and the field vole *Microtus agrestis* are also referred to. We attempt to verify the general validity of the model and present some new data on the impact of kinship and familiarity on the population growth in cyclic bank vole (*Clethrionomys glareolus*) populations.

Differences between cyclic *Clethrionomys* and *Microtus agrestis* populations

One main point of criticism for the Lambin-Krebs model is that it cannot be valid for all microtines. In Fennoscandia there are distinct differences in the annual social organization between *Clethrionomys* and *Microtus* voles. Nevertheless, the long-term population fluctuations — especially the decline phases — are synchronous in all species (Henttonen et al. 1987). We have carried out several long-term comparative studies and experiments on social organization of the bank vole (*Clethrionomys glareolus*) and the field vole (*Microtus agrestis*) in Central Finland (Ylönen 1990; Ylönen et al. 1988, 1990; Ylönen & Viitala 1985, 1991, 1993; Puseenius & Viitala 1993a, b). On the basis of these studies we can describe the annual change in the social structure — including information on kin interactions — of the populations in relation to the phase of the cycle. The studies on the bank vole were conducted in large outdoor enclosures. Since the enclosure populations of *Clethrionomys* did not show any overcrowding effects ("Fence-effect", see. Boonstra & Krebs 1977, and Ylönen et al. 1988), we believe it is justified to use the enclosure data in the present paper.

In Fennoscandia voles of both the genera *Clethrionomys* and *Microtus* seem to overwinter mainly in aggregations (Myllymäki 1977, Ylönen & Viitala 1985). However, in the field vole the aggregations seem to be larger and less stable due to exhaustion of resources around the aggregation. This results in lower winter survival in *Microtus* than in *Clethrionomys*, the under-snow survival of which is normally very high (Ylönen & Viitala 1985). After the spring thaw we have observed only little or no spring decline in cyclic populations compared to non-cyclic ones (c.f. Krebs & Myers 1974), as also stated by Lambin & Krebs (1991). A possible spring decline could be due to predation, occurrence of diseases and/or microparasites (Henttonen & Haukialmi, pers. comm.) or severe environmental conditions — thawing by day and freezing by night (Heikura 1977) — rather than to social reasons.

The Lambin-Krebs model assumes a decrease in the degree of relatedness between females in spring to be the cause for the increasing competition for space and for the strong spring decline. In the bank vole we have found no evidence for winter dispersal of females (possible also in the enclosure populations due to high snow cover) nor severe competition for space in spring which should lead to a decrease of female relatedness in the beginning of the breeding season. In *Clethrionomys* after the formation of spring territories there still remains “free” space between the female home ranges (Table 1). In a long term enclosure study (Ylönen 1990, Ylönen et al. 1988) the spring home range (HR) size varied significantly along the cycle (Table 1, Kruskal-Wallis oneway ANOVA, $H = 11.3$, $P = 0.01$) so that the HR was at its largest during an increase year. However, there was no significant difference between a prepeak in spring 1985, with a high female density, and a precrash in spring 1986 with a moderate female density (Table 1, two-sample $t = 0.35$, $P = 0.73$). The space use pattern of female bank voles in spring, determined as the percentage of the area used by the females from the total area of the enclosure, and the HR overlap between females (Table 1) does not support ideas of the lack of space and severe competition for territories. In the field vole both sexes can disperse during winter (Myllymäki 1977). Together with winter mortality this could lead to

space competition in the most optimal habitat patches, and to stronger spring declines than in *Clethrionomys* populations.

Lambin & Krebs' (1991) suggestions that a high female density in spring should ultimately lead to a high summer density is not supported by our long-term data on cyclic bank vole or red vole *Clethrionomys rutilus* (Viitala 1987) populations. A moderate female bank vole density in the spring 1984 was followed by a peak in August, the same spring density by a crash in 1986. The degree of familiarity between the enclosure females after having spent the winter in aggregations was high in both years and no females could immigrate into the population in spring. All females of the crash spring had their first litters early but the survival of the young was low (Ylönen et al. 1988) suggesting that extrinsic factors caused the deep decline of the population during the following summer. Further, in an enclosure population the degree of relatedness between females cannot decrease in spring due to restricted immigration of strange animals. Thus according to the Lambin-Krebs model the same spring density with the same average degree of relatedness/familiarity should have produced similar summer densities, which was not the case (Table 1, Ylönen et al. 1988). On the other hand Viitala (1987) observed in a free-living population of *Clethrionomys rutilus* a peak summer density after an exceptionally high exchange rate of individuals in the preceding winter and a decline after a winter with only little changes in the overwintering population.

In two experiments we have shown that both relatedness and familiarity between the individuals increase population growth in the first half of the breeding season (Ylönen et al. 1990, Fig. 1). Thus the familiarization of the individuals forming the winter aggregations already promotes the survival of the young born in spring. Of the two kinship seems to have a stronger effect on the growth rate (Fig. 1) but the difference is not big. There does not exist any field data on the kin composition of winter aggregations, but it seems obvious that a female born during the preceding spring together with its last litter form the basic unit of an aggregation. Our results on the bank vole support the basic assumption of the Lambin-Krebs model that the higher the degree of

relatedness in the spring breeding unit the higher the growth rate of the population. Further our data supports the correlation between winter breeding and population peak in the following summer (Table 1) as suggested by the model. However, we believe that this is caused by a good food situation and an increased number of litters per breeding season (Ylönen et al. 1988) and not due to increased degree of relatedness in the spring population after winter breeding.

Conclusions

Although we have found little support for some of the assumptions made by Lambin & Krebs (1991) we agree with their main assumption that the degree of relatedness (and/or familiarity) can promote population growth in at least some species. In our experiments we have been able to show the positive impact of the high degree of kinship and familiarity on the population growth in a controlled predator-free environment (Ylönen et al. 1990, Fig. 1). It has been shown that both the bank vole and the field vole usually overwinter in social aggregations which promotes the matching of an individual female to conspecifics which will surround her in the beginning of the breeding season. This already seems to be enough to decrease the level of agonistic interactions and to increase juvenile survival compared to socially more heterogenous breeding populations, at least in the bank vole (Fig. 1). The kind of “dilution”

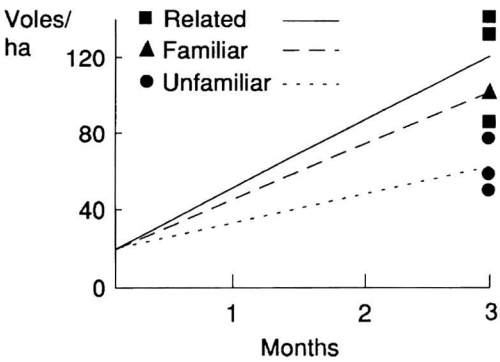


Fig. 1. Growth of bank vole (*Clethrionomys glareolus*) populations with different origin of the founder population in June. The data comes from two three-month experiments with known degree of relatedness (3 populations) and familiarity (one population) of the founder individuals compared to populations founded of unfamiliar females (3 populations). The results show that both relatedness and mutual familiarity have a positive impact on the growth of the population compared to a heterogenous founder population, but that the impact of kinship is still stronger.

of female spring populations due to winter predation and subsequent movements of “surplus females” as suggested by the Lambin-Krebs model could be true for some *Microtus* species but not for any of the *Clethrionomys* species studied so far.

The main disagreement between us and the Lambin-Krebs model is probably the role of extrinsic factors in the demographic patterns, which is the basic question in understanding the cyclic

Table 1. Density and spatial distribution of female *Clethrionomys glareolus* in spring at the onset of breeding in a 0.8-ha enclosure at Konnevesi, Central Finland. Home range (= HR with SD) size is defined as 100 m² multiplied by the average number of the trap sites used by a female during ten trap checkings, HR overlap is the percentage of the traps used by two or more females, Space use is the percentage of the trap sites used by the females (of the total number of 81 sites in the enclosure), Peak density is voles/ha in August, and Phase is a characterization of the year in the long-term cyclic dynamics. The years with winter breeding are denoted with an asterisk.

	Females	HR size	HR overlap	Space use	Peak density	Phase
March 1984 *	9	233 ± 111	22	22	145	Peak
March 1985	21	330 ± 44	38	61	117	Peak
March 1986	9	311 ± 16	22	28	5	Crash
Feb-March 87 *	4	575 ± 25	46	19	43	Increase

vs. non-cyclic population fluctuations (cf. Krebs & Myers 1974 vs. Hansson & Henttonen 1988, Hanski et al. 1991). We suggest that the environmental conditions around a breeding unit — including climatic factors, predation, as well as the occurrence of diseases and parasites — turn the populations of different species to a strict synchronous decline. However, the increase phase of the populations is much less synchronous and there such factors as relatedness between the individuals could play different roles in different species. Predation is included in the Lambin-Krebs model only as a factor contributing to the social cohesion of the spring population. According to our experience on the causes of summer declines in the microtine populations this is a total underestimation of the general impact of predation (Henttonen et al. 1987, Hanski et al. 1991) and the additional indirect effects of predators in deepening the population declines (Ylönen et al. 1992).

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