

Review

Impact of kinship and familiarity on the annual social organization and population dynamics of *Clethrionomys* and *Microtus* voles

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In the following we review the results of comparative and experimental studies on the impact of kinship and familiarity on the social systems and population dynamics of microtine rodents. We refer especially to the bank vole *Clethrionomys glareolus* and the field vole *Microtus agrestis*. In the beginning of the breeding season the neighbouring territorial *Clethrionomys* females can be close kin or at least mutually familiar after having spent the winter in an aggregation and probably having nested together. This relatively high degree of kinship or familiarity promotes population growth in the first half of the breeding season, if external factors, such as food and predation, allow it. Kinship should have less or no impact on the social relationships in *Clethrionomys* males. The impact of relatedness between the breeding females seems to be unimportant in *Microtus agrestis*. The differences in kin interactions between these species are most probably food-mediated. Field voles use most effectively the rich food resources during the early summer. The preferred dicotyledons are, however, soon depleted and the growth of the graminids slows down as they form seeds during midsummer. As a consequence the breeding females have a strong tendency to disperse and kin groups are very short-lived. This affects the population density negatively during mid-summer. In the bank vole females the lower level of agonism among neighbouring breeding females promotes population growth but exclusive female territoriality throughout the breeding season prevents as a rapid population growth as in the field vole. The role of kin interactions in population dynamics of *Clethrionomys* and *Microtus* voles seems to be different, but as a whole it should have an annual character only, and have no or little to do with multiannual population fluctuations of microtine rodents.

1. Introduction

Questions on the impact of relatedness to population parameters have been a subject of intense research and discussion since the kin selection theory by Hamilton (1963, 1964, 1970). Kin selection studies first concerned on the problems of relationship between altruistic behaviour and inclusive fitness of individuals. A decade ago they produced promising hypotheses to explain cyclic population fluctuations of small rodents — one of still existing challenges of population ecological research (Lidicker 1988). One of the most discussed and tested hypothesis has been that of Charnov and Finerty (1980). It suggests that the individuals during a low population density are surrounded by related animals, behave amicably towards each other and this promotes the growth of the population. Inversely, the individuals of a high density population are more likely surrounded by non-relatives, which is expressed by a high degree of aggressiveness between them and leads to the decline of the population density.

After ten years discussions Charnov and Finerty hypothesis has been shown to be insufficient to explain cyclic multiannual population fluctuations (e.g. Pugh & Tamarin 1990, Stenseth & Lomnicki 1990). However, it has initiated a number of field and laboratory studies on the relationship between relatedness and population growth (Boonstra & Hogg 1988, Ylönen et al. 1990, review by Kawata 1990, Lambin & Krebs 1993, Sera & Gaines 1994), but also on the impact of kinship and familiarity on social processes and reproductive success (Armitage 1990, Ferkin 1990, Mappes et al. 1995).

The aim of the present paper is to review mainly our own long-term studies on the relationship between the social organization and demography in cyclic microtine populations in northern and central Fennoscandia. We describe the patterns of social organization and the impact of relatedness and familiarity on annual social systems and demography of *Clethrionomys* and *Microtus* voles. Bank voles and field voles exploit different habitats and should exhibit different life-historical adaptations to annually changing environmental conditions (Viitala 1977, Ylönen 1989a, Pusenius and Viitala 1993a, b). In

this paper we review some of the recent experimental studies, too. We also point out the importance of long-term comparative data collection (Haila 1988). It is the way to understand the plasticity in the responses of individuals and populations to changes in annually and multi-annually changing social environment.

2. Study areas and material

We have conducted several long term studies in northern and central Finland on social adaptations of individuals and populations during different phases of the population cycle of microtines. We view the changing social behaviour of individuals and the organization of populations as an adaptation to environmental conditions (Ylönen 1989a, 1990, Viitala & Ylönen 1993).

Our material consists of studies in northern Finland in 1964–74. They dealt with two *Clethrionomys* species, *C. rufocanus* and *C. rutilus* (Viitala 1977, 1987) and one *Microtus* species, *M. agrestis* (Viitala 1977). The material from central Finland consists of comparative studies on *Clethrionomys glareolus* (Ylönen & Viitala 1985, Ylönen et al. 1988) and introduced *C. rufocanus* (Ylönen & Viitala 1987) in 1982–88. Comparative studies on *Microtus agrestis* from central Finland (Pusenius 1992, Pusenius & Viitala 1993a, b) compile the material of this interspecific comparison. In all of the mentioned studies the method has been capture-mark-recapture (CMR) and the field work has been carried out by the same persons so that the comparability of the studies is best possible. In the reviewed papers we determined following factors in order to describe the population structure: an index of the size of individual home ranges (determined as a number of used trap sites during one trapping period), formation of family clans, movements of young from the natal home range to the breeding home range, consistency of sibling groups and intersexual differences in the space use. In central-Finnish studies live-trapping was conducted during the winters, too. We review also some data on our field experiments carried out in either four 0.5 ha enclosures or in eight 0.25 ha enclosures (Ylönen et al. 1990, Ylönen & Viitala 1991, Pusenius 1993, Pusenius & Viitala 1995).

3. Kinship and familiarity vs. annual social structure and population dynamics in *Clethrionomys*

The population density of the bank vole (*Clethrionomys glareolus*) fluctuated during our six-year enclosure study in central Finland similarly as described, e.g. by Hansson and Henttonen (1988) for

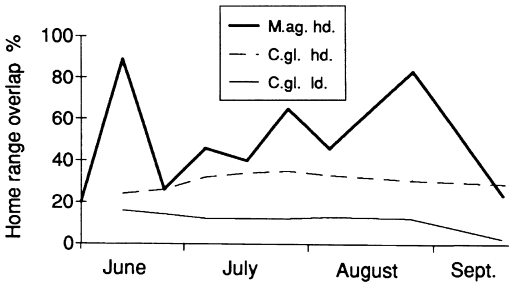


Fig. 1. Differences in the home range overlap of breeding bank vole females during the moderate density summer 1984 and high-density breeding season 1985 (thin lines, according to Ylönen et al. 1988) and during a high-density summer 1985 in the field vole (thick line, According to Pusenius & Viitala 1993b).

cyclic populations. We had population crashes 1982 and 1986, and in-between an increase year and two peak years (Ylönen et al. 1988). The average home range size of breeding females was largest (630 m²) during the increase phase of the population cycle in 1983. During all other phases of the cycle the home range size did not vary considerably and was under 500 m² (Ylönen 1990). Home range overlap during the breeding season was affected by density (Fig. 1). The maximum was 37% during a high density of breeding females in 1984 (Ylönen et al. 1988, Ylönen 1990). The overlap was always high during the non-breeding season (Ylönen & Viitala 1985, Ylönen 1990). We observed the same pattern for the grey-sided vole (*C. rufocanus*) population, which originated 700 km farther north and was introduced to an island in central Finland (Ylönen & Viitala 1987). In the bank vole the home range overlap decreased with increasing population density during the high density breeding seasons 1984 and 1985. This may indicate a density-mediated more aggressive defence of the home range, either as a food resource (e.g. Ylönen et al. 1988) or as a safe nest sites for defending of the young (Wolff 1993).

The common pattern of over-wintering in central and southern Fennoscandian *Clethrionomys* populations seems to be an intersexual aggregation or a small group (Fig. 2, Ylönen & Viitala 1985, Karlsson 1988). This was verified experimentally, too (Ylönen & Viitala 1991, H. Ylönen & T. Mappes, unpubl). It has been suggested that aggregative behaviour would be dependent on the abundance and distribution of winter food

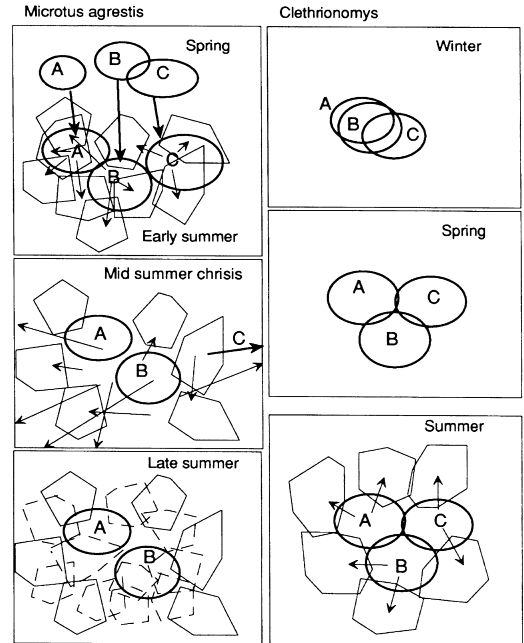


Fig. 2. Schematic presentation of seasonal changes in the social organization of female field voles and bank voles. Seasonal movements of individuals are indicated by arrows. Ellipses = overwintered females, polygons = first cohort females, broken line = second cohort female field voles. The main features in the *Microtus* system are the only short lived kin-clusters throughout the breeding season, adult female dispersal during midsummer and relatively stochastically formed associations (according to Viitala 1977 and Pusenius and Viitala 1993b). The main features in the *Clethrionomys* system are aggregative behaviour in winter and philopatry of both overwintered females after splitting of the aggregation in spring and of daughters during early summer (according to Ylönen & Viitala 1985 and Ylönen et al. 1988).

(West & Dublin 1984) so that under poor food circumstances voles could occupy exclusive winter territories. An indication of this could be the dispersing of young grey-sided voles to individual territories just before the onset of winter at Kilpisjärvi, north-western Lapland (Viitala 1977) but actual winter studies are lacking. However, at Pallasjärvi, Forest-Lapland, concentration sites of *Clethrionomys* home ranges in winter could not be found (Henttonen & Viitala 1983).

One crucial factor in the social overwintering of voles should be heat-saving when nesting

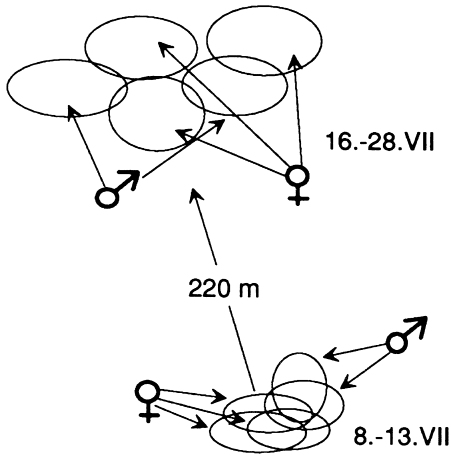


Fig. 3. An example of the group dispersal of in the grey-sided vole siblings (three females and two males) between the trappings of two consecutive weeks observed in summer 1974 at Kilpisjärvi, Finnish Lapland.

communally (Sealander 1952, Vickery & Millar 1984). An aggregation — or a smaller group — in a field population consists normally of two to four females and one or two males (Karlsson 1988). With experimental increasing of local food resources the number of joining individuals can be increased to upto 10 per one group (Ylönen & Viitala 1991). Overwintering aggregations are often formed by 1–2 neighbouring females with some of the last litter young staying in the group or its vicinity. Males joining the group seem to be unrelated to the females in the group (Ylönen & Viitala 1985). Group movements of siblings are common. Often 3–5 young bank voles of the same litter are captured in the same live-trap (H. Ylönen et al., unpubl. data). The same is true for the more northern grey-sided vole. In this species we witnessed a sibling dispersal over great distances between the capture co-ordinates of two consecutive trapping periods (Fig. 3, J. Viitala, unpubl. data). This kind of late summer sibling groups can obviously form over wintering groups, too. In total, relatedness between neighbouring individuals, whether over wintering in groups or not, should therefore be high. Also the joining unrelated individuals have a long non-breeding season with low level of ag-

gressiveness to get familiar with other members of the group. Thus they possibly benefit of the familiarity and increased mutual tolerance in the beginning of the next breeding season. Territorial females during the breeding season seem to form the basic social structure of *Clethrionomys* populations. Therefore the impact of possible kin-recognition and familiarisation should be of greater importance for females than for males (Ylönen et al. 1988, Ferkin 1990, Ylönen 1990).

In spring by the onset of breeding the (female) aggregations split apart. However, the breeding territories are formed as close to the over wintering site as possible (Fig. 2, Ylönen et al. 1988, see Viitala 1987 for an exception). During a winter with abundant food female bank voles can exceptionally already be pregnant when moving to the breeding territory (Ylönen & Viitala 1985). Kinship and/or familiarity together with rich food resource (exceptional seed crop of spruce and alder in winter 1984) can strongly alter the normally observed breeding territoriality of bank vole females. In spring 1984 breeding started very early under the snow and females from the same winter group reproduced on greatly overlapping breeding territories and despite this the survival of the young until breeding age was 100% (Ylönen & Viitala 1985). Females of the first litter disperse shortly after they have been weaned but stay as close to the natal home range as possible (Fig. 2). In moderate density year 1982 the average distance moved between natal and breeding territory was 40 metres (Ylönen et al. 1988). These females of the first litters become mature and breed during their first summer already. Thus the degree of kinship between neighbouring breeding females remained fairly high during at least the first half of the breeding season. In behavioural trials with mothers and their daughters that had already founded an own territory and were pregnant we recognized that the degree of aggressiveness was lower among kin than in non-kin female-female pairs used for comparison (H. Ylönen, unpubl. data). We could also experimentally verify the prediction that kinship and familiarity increase the growth rate of bank vole populations (Ylönen et al. 1990).

As space becomes limited during the latter part of the summer the next litters have two choices: either to disperse farther, separately or

in sibling groups (Fig. 3.) and find a breeding territory already during the summer of birth, or to stay immature in the natal home range and wait for the next breeding season. We have mainly been working with enclosure and island populations. Thus we have been unable to determine the mode and effects of dispersal, except for one unreplicated experiment. It showed a great difference in the age and sexual status of dispersers between *Clethrionomys* and *Microtus* voles (Viitala et al. 1994). That submature bank voles are capable for probably very costly long-term dispersal was verified during the island study of the grey-sided vole (*C. rufocanus*). Every summer between 1983 and 1986 some young bank voles (maximum seven in high-density year 1985) reached the Iso-Korppi island (ca. 400 metres from a larger island near mainland) by swimming. The more closely to the continent situated Siimari-Island (ca. 80 metres from mainland) was rapidly recolonized by the bank vole after the disappearance of grey-sided voles from the island (Ylönen & Viitala 1987). One could predict that the stronger long-distance dispersal during the latter part of the breeding season could increase the heterogeneity of populations as suggested by Charnov and Finerty (1980). However, we believe that the sibling group dispersal of voles is more common than expected until now. It would explain the observations by Pugh and Tamarin (1990) that the degree of relatedness in a population of *Microtus pennsylvanicus* did not deviate between low and high density years.

On the other hand one might ask what are the benefits of agonistic interactions between mutually unfamiliar individuals? One could assume that in a heterogeneous population established by long-term dispersal, agonistic interactions could keep the density below the carrying capacity of the suboptimal habitat (the optimal habitat is already occupied). This could promote survival of individuals forced to use the marginal habitat. We suggest that the basic social structure of *Clethrionomys* voles is a matriarchat where kin interactions play a strong role as long as environmental factors allow population growth. Strong seasonality and periodicity in predation pressure seem to be the "Zeitgebers" of the population dynamics determining the shape of long term population fluctuations.

4. Kinship, familiarity, social structure and reproductive success in *Microtus agrestis*

There is not much information on the social overwintering of *Microtus* from the areas where there is a permanent snow cover in winter. Studies of Myllymäki (1977) with a confined colony indicate that field voles (*Microtus agrestis*) form aggregations where they are capable of huddling together. These aggregations seem, however, to be random and can change both members and location in time. Pusenius (1992) found in an open population that field voles lived mostly in aggregations until December. Since January there was a tendency to live more separately. The breakdown of the aggregations occurred simultaneously with a marked loss of individuals from the population.

Winter survival of *Microtus* seems to be considerably lower than that of *Clethrionomys*. Viitala (1977, 1984) found in an open northern Finnish study plot that survival during a peak year winter was 46% for *C. rufocanus* and 26% for *M. agrestis*. In a study with open central Finnish peak year populations Pusenius (1992) estimated a winter survival of 49% for *C. glareolus* and 15% for *M. agrestis*. The trapping grid consisted partly forest and partly old field. The field voles living on the old field side were exposed to a heavier predation pressure indicated by the abundance of weasel tracks (J. Pusenius, unpubl.).

If the increased degree of relatedness promotes the survival of the population during the non-breeding season in the same way as during the breeding season (e.g. Lambin & Krebs 1993), its effect may not be very important in *Microtus*. That is because of the random nature of the overwintering aggregations and the importance of other mortality factors such as predation at least during some years. It seems that the mortality rate in *Microtus* voles is more density dependent during the winter than in the bank vole.

During the breeding season young field vole females mature already on the home range of their mother (Viitala 1977). Lambin and Krebs (1991) argued that in this kind of situation kin clusters of breeding females are formed due to philopatry of female voles. This does not, however, happen in *Microtus agrestis*. We used

radionuclides to determine matrilineal kinship (Pusenius 1993). We found that the associations between the mother and the daughter were very short-lived and living in a kin association did not enhance reproductive success. The young females that had their mother as their nearest neighbour got the same number of trappable recruits as the young females that had a strange old female as their nearest neighbour. Furthermore, familiarity between neighbouring breeding field vole females does not seem to have an effect on their spacing behaviour and reproductive success. Pusenius and Viitala (1995) made an experiment with *M. agrestis* using similar design as that of Ylönen et al. (1990) with *C. glareolus*: populations of familiar and related individuals were compared with populations of unrelated and strange individuals. The difference between the species was clear. Unlike in *Clethrionomys* no behavioural or demographical differences between the treatments were found in *Microtus agrestis*. In the familiarity and kin treatment the coefficient of kinship was somewhat lower in the *Microtus* experiment than in the *Clethrionomys* one. However, familiarity and not the coefficient of kinship has been found to be the more important factor determining the nature of the social interactions in rodents (see, e.g. Bekoff 1981, König 1994).

Thus kinship or familiarity does not seem to affect social behaviour or reproductive success in *Microtus agrestis* during the breeding season. This is at least partly due to the dispersal tendency of the older breeding females probably connected to availability of high quality food. Although old field is a very productive habitat, the preferred dicotyledons are soon depleted and the growth of the graminids slows down as they form the seeds in midsummer (Myllymäki 1977). The following dispersal breaks down associations between neighbouring kin and may even reduce population density (Myllymäki 1977, Pusenius 1993, Pusenius and Viitala 1993a).

5. Conclusions

The impact of kinship on the population structure and growth seems to be different in *Clethrionomys* and *Microtus* voles. This was exactly what we have expected on basis of previously known differences

in the ecology of these two genera (Viitala & Hoffmeyer 1985, Ylönen et al. 1995), with some exceptions in North-American *Microtus* species. *Clethrionomys* voles inhabit relatively stable forested habitats with restricted food resources of seeds, buds, fungi and herbs (Hansson 1985) both during summer and winter. They have evolved a relatively stable social system basing on female territoriality (Kalela 1957). This kind of environment does not support as great population outbreaks as a field or meadow, where green biomass accumulates rapidly during early summer. In the stable *Clethrionomys* system kin interactions could have a greater impact on population processes than in the *Microtus* system. The social organization in field voles reflects their “explosive” reproduction during the growth of fresh, green plant material. It is followed by dispersal to new breeding grounds as the high quality food is depleted (Myllymäki 1977).

If the high degree of relatedness and/or familiarity decreases aggressiveness between the neighbouring females — leading to a lower degree of infanticide (e.g. Boonstra 1984, Wolff 1985) — this should promote the growth of the population. This was evident in an experiment with the bank vole (*C. glareolus*) but not with *M. agrestis* and in two North-American studies on *Microtus* voles (Boonstra & Hogg 1988, Sera & Gaines 1994). However, Boonstra & Hogg’s study was unreplicated and recently Wolff (1995) criticised the other *Microtus* study of using unfamiliar males in the experimental “Friends” populations with high degree of kinship among females only. This could increase the probability of male infanticide and be reflected in the slower population growth of the populations founded by kin females, too. Due to different exploitation of available resources in *Clethrionomys* and *Microtus* voles relatedness and familiarization could have a different impact in shaping social interactions among individuals of these species. A slower growth rate and social stability in “forest voles” and high rate of harvesting of green biomass, rapid population growth and social instability in “field voles” would reflect these differences.

Finally, back to the idea paper by Charnov and Finerty (1980). There are strong indications that increased degree of kinship in a population could promote survival of the young produced. This could lead to a rapid population growth —

at least in some species and under certain environmental conditions. Nobody, however, has been able to show that an inverse development of relatedness along the population growth would bring the population to decline. Further, Pugh and Tamarin (1990) could show that the degree of relatedness did not differ between the years of low and a high density in their study population. We suggest that at least in *Clethrionomys* voles kin interactions can promote annual population growth during low and moderate density springs. During high density years external factors most probably overwhelm the impact of kin interactions and familiarity in determining the population structure and growth. Such factors include exploitation of local food resources, length of snowy period, characteristics of the spring thaw in Fennoscandia, and the changing assemblage of parasites, pathogens and predators (Hansson & Henttonen 1988, Ylönen 1989b, 1994, Hanski et al. 1991, Haukialmi 1991).

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References

- Armitage, K. B. 1987: Social dynamics of mammals: Reproductive success, kinship and individual fitness. — *Trends Ecol. Evol.* 2: 279–284.
- Bekoff, M. 1981: Vole population cycles: kin-selection or familiarity? — *Oecologia* 48: 131.
- Boonstra, R. 1984: Aggressive behavior of adult meadow voles (*Microtus pennsylvanicus*) towards young. — *Oecologia* 62: 126–131.
- Boonstra, R. & Hogg, I. 1988: Friends and strangers: a test of the Charnov-Finerty Hypothesis. — *Oecologia* 77: 95–100.
- Charnov, E. L. & Finerty, J. P. 1980: Vole cycles: a case for kin-selection? — *Oecologia* 45: 1–2.
- Ferkin, M. H. 1990: Kin recognition and social behaviour in microtine rodents. — In: Tamarin, R. H., Ostfeld, R. S., Pugh, S. R. and Bujalska, G. (eds.), *Social systems and population cycles in voles*. Birkhäuser Verlag, Basel, pp. 11–24.
- Haila, Y. 1988: The multiple faces of ecological theory and data. — *Oikos* 53: 408–414.
- Hamilton, W. D. 1963: The evolution of altruistic behaviour. — *Am. Nat.* 97: 354–356.
- Hamilton, W. D. 1964: The genetic evolution of social behaviour. — *J. Theor. Biol.* 12: 1–52.
- Hamilton, W. D. 1970: Selfish and spiteful behaviour in an evolutionary model. — *Nature* 228: 1218–1220.
- Hanski, I., Hansson, L. & Henttonen, H. 1991: Specialist predators, generalist predators, and the microtine rodent cycle. — *J. Anim. Ecol.* 60: 353–367.
- Hansson, L. 1985: The food of bank voles, wood mice and yellow-necked mice. — *Symp. Zool. Soc. Lond.* 141–168.
- Hansson, L. & Henttonen, H. 1988: Rodent Dynamics as Community processes. — *Trends Ecol. Evol.* 3: 195–200.
- Haukialmi, V. 1991: Commonness and rarity in parasitic helminths of voles. — Ph. D. Dissertation, Univ. of Helsinki.
- Henttonen, H. & Viitala, J. 1983: Aspects of the social behaviour of cyclic microtines in winter. — *Oulanka Reports* 4: 79–81. (In Finnish, with an English abstract).
- Kalela, O. 1957: Regulation of reproduction rate in subarctic populations of the vole *Clethrionomys rufocanus* (Sund.). — *Ann. Acad. Sci. Fennicae A IV*: 1–60.
- Karlsson, A. F. 1988: Social organization of a low density spring population of the bank vole, *Clethrionomys glareolus*. — *Oikos* 52: 19–26.
- Kawata, M. 1990: Fluctuating Populations and Kin Interaction in Mammals. — *Trends Ecol. Evol.* 5: 17–20.
- König, B. 1994: Fitness effects of communal rearing in house mice: the role of relatedness versus familiarity. — *Anim. Behav.* 48: 1449–1457.
- Lambin, X. & Krebs, C. J. 1991: Can changes in female relatedness influence microtine population dynamics? — *Oikos* 61: 126–132.
- Lambin, X. & Krebs, C. J. 1993: Influence of female relatedness on the demography of Townsend's vole populations in spring. — *J. Anim. Ecol.* 62: 536–550.
- Lidicker, W. Z. Jr. 1988: Solving the enigma of microtine "cycles". — *J. Mamm.* 69: 225–235.
- Mappes, T., Ylönen, H. & Viitala, J. 1995: Higher reproductive success among kin groups of bank voles *Clethrionomys glareolus*. — *Ecology*. (In press).
- Myllymäki, A. 1977: Intraspecific competition and home range dynamics in the field vole *Microtus agrestis*. — *Oikos* 29: 553–569.
- Pugh, S. R. & Tamarin, R. H. 1990: A test of Charnov and finerty hypothesis of population regulation in meadow voles. — In: Tamarin, R. H., Ostfeld, R. S., Pugh, S. R. & Bujalska, G. (eds.), *Social systems and population cycles in voles*: 11–24. — Birkhäuser Verlag: Basel–Boston–Berlin.
- Pusenius, J. 1992: Space use and winter survival of the voles *Microtus agrestis* and *Clethrionomys glareolus* in Central Finland. — 4th Int. Beh. Ecol. Congr. Princeton 17–22 Aug. 1992, Abstracts P 68.
- Pusenius, J. 1993: Matrilineal kin clusters and their effect on reproductive success in the field vole *Microtus agrestis*. — *Mammalia* 57: 643.
- Pusenius, J. & Viitala, J. 1993a: Demography and regulation of breeding density in the field vole, *Microtus agrestis*. — *Ann. Zool. Fennici* 30: 133–142.
- Pusenius, J. & Viitala, J. 1993b: Varying spacing behaviour of breeding field voles, *Microtus agrestis*. —

- Ann. Zool. Fennici 30: 143–152.
- Pusenius, J. & Viitala, J. 1995: Familiarity of breeding field vole (*Microtus agrestis*) females does not affect their space use and demography of the population. — Ann. Zool. Fennici 32: 217–223.
- Sealander, J. A. 1952: The relationship of nest protection and huddling to survival of *Peromyscus* at low temperature. — Ecology 33: 63–71.
- Sera, W. E. & Gaines, M. S. 1994: The effect of relatedness on spacing behavior and fitness of female prairie voles. — Ecology 75: 1560–1566.
- Stenseth, N. C. & Lomnicki, A. 1990: On the Charnov-Finerty hypothesis: the unproblematic transition from docile to aggressive and the problematic transition from aggressive to docile. — Oikos 58: 234–238.
- Vickery, W. L. & Millar, J. 1984: The energetics of huddling by endotherms. — Oikos 43: 88–93.
- Viitala, J. 1977: Social organization in cyclic subarctic populations of the vole *Clethrionomys rufocanus* (Sund.) and *Microtus agrestis* (L.). — Ann. Zool. Fennici 14: 53–93.
- Viitala, J. 1984: Stability of overwintering populations of *Clethrionomys* and *Microtus* at Kilpisjärvi, Finnish Lapland. — Spec. Publ. Carnegie Mus. Nat. Hist. 10: 109–112.
- Viitala, J. 1987: Social organization of *Clethrionomys rutilus* (Pall.) at Kilpisjärvi, Finnish Lapland. — Ann. Zool. Fennici 24: 267–273.
- Viitala, J. & Hoffmeyer, I. 1985: Social organization in *Clethrionomys* compared with *Microtus* and *Apodemus*: social odours, chemistry and biological effects. — Ann. Zool. Fennici 22: 359–371.
- Viitala, J. & Pusenius, J. 1990: A comparative study of phenotypic changes in *Microtus* social organization. — In: Tamarin, R. H., Ostfeld, R. S., Pugh, S. R. & Bujalska, G. (eds.), Social systems and population cycles in voles: 131–142. Birkhäuser Verlag: Basel-Boston-Berlin.
- Viitala, J. & Ylönen, H. 1993: From population dynamics to experimental evolutionary ecology: causes and consequences of social processes in voles. — Ann. Zool. Fennici 30: 177–186.
- Viitala, J., Hakkarainen, H. & Ylönen, H. 1994: Different dispersal in *Clethrionomys* and *Microtus*. — Ann. Zool. Fennici 31: 411–415.
- West, S. D. and Dublin, H. T. 1984: Behavioral strategies of small mammals under winter conditions: solitary or social? — Special Publication Carnegie Museum of Natural History: 293–299.
- Wolff, J. O. 1985: Maternal aggression as a deterrent to infanticide in *Peromyscus leucopus* and *P. maniculatus*. Anim. Behav. 33: 117–123.
- Wolff, J. O. 1993: Why are small mammals territorial. — Oikos 68: 364–370.
- Wolff, J. O. 1995: Friends and strangers and vole cycles. — Oikos (in press).
- Ylönen, H. 1989a: Temporal variation of behavioural and demographical processes in cyclic *Clethrionomys* populations. — Biol. Res. Rep. Univ. Jyväskylä 16: 1–35.
- Ylönen, H. 1989b: Weasels *Mustela nivalis* suppress reproduction in cyclic bank voles *Clethrionomys glareolus*. — Oikos 55: 138–140.
- Ylönen, H. 1990: Phenotypic flexibility in the social organization of *Clethrionomys*. — In: Tamarin, R. H., Ostfeld, R. S., Pugh, S. R. & Bujalska, G. (eds.), Social systems and population cycles in voles: 203–212. — Birkhäuser Verlag: Basel-Boston-Berlin.
- Ylönen, H. 1994: Vole cycles and antipredatory behaviour. — Trends Ecol. Evol. 9: 226–230.
- Ylönen, H. & Viitala, J. 1985: Social organization of an enclosed winter population of the bank vole *Clethrionomys glareolus*. — Ann. Zool. Fennici 22: 353–358.
- Ylönen, H. & Viitala, J. 1987: Social organization and habitat use of introduced populations of the Vole *Clethrionomys rufocanus* (Sund) in Central Finland. — Z. Säugetierkd. 52: 354–363.
- Ylönen, H. & Viitala, J. 1990: Kin interactions and population growth. — Trends Ecol. Evol. 5: 371.
- Ylönen, H. & Viitala, J. 1991: Social overwintering and food distribution in the bank vole *Clethrionomys glareolus*. — Holarct. Ecol. 14: 131–137.
- Ylönen, H., Kojola, T. & Viitala, J. 1988: Changing female spacing behaviour and demography in an enclosed breeding population of *Clethrionomys glareolus*. — Holarct. Ecol. 11: 286–292.
- Ylönen, H., Mappes, T. & Viitala, J. 1993: Female relatedness and microtine population dynamics: experience from cyclic populations. — Ann. Zool. Fennici 30: 77–80.
- Ylönen, H., Koskela, E. & Mappes, T. 1995: Small mustelids and breeding suppression of cyclic microtines: adaptation or general sensitivity. — Ann. Zool. Fennici 32: 171–174.
- Ylönen, H., Mappes, T. & Viitala, J. 1990: Different demography of friends and strangers: an experiment on the impact of kinship and familiarity in *Clethrionomys glareolus*. — Oecologia 83: 333–337.