



Nordic Society Oikos

Can Changes in Female Relatedness Influence Microtine Population Dynamics?

Author(s): Xavier Lambin and Charles J. Krebs

Source: *Oikos*, Vol. 61, No. 1 (May, 1991), pp. 126-132

Published by: [Blackwell Publishing](#) on behalf of [Nordic Society Oikos](#)

Stable URL: <http://www.jstor.org/stable/3545414>

Accessed: 06/01/2011 20:58

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=black>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Blackwell Publishing and *Nordic Society Oikos* are collaborating with JSTOR to digitize, preserve and extend access to *Oikos*.

<http://www.jstor.org>

Can changes in female relatedness influence microtine population dynamics?

Xavier Lambin and Charles J. Krebs, *The Ecology Group, Dept of Zoology, Univ. of British Columbia, Vancouver, B. C., Canada V6T 2A9 (XL also: Unité d'Ecologie et de Biogéographie, Univ. Catholique de Louvain, B-1348 Louvain-la-Neuve, Belgium.*

We present a model relating fluctuations in density of vole and lemming populations to changes in the degree of relatedness among females. We propose that a high degree of relatedness prior to the spring decline causes more overlap between female home ranges and leads to a high density of breeding females in spring and vole outbreak densities in summer. Low relatedness in spring leads to competition for territories between females and to a severe spring decline. We suggest that severe mortality owing to predators or reduced mortality resulting from favorable environmental conditions that allow winter breeding may influence the genetic structure of a population and thus the intensity of competition for space among females. The predictions of our model are opposite to those of the Charnov-Finerty (1980) model. Charnov and Finerty predicted that the degree of relatedness would be inversely correlated with population density and that a decline in degree of relatedness at high density causes population crashes. We predict that relatedness fluctuates seasonally and is greatest at high density owing to the philopatry of juvenile females. We also predict that declines in relatedness are due to predation and immigration during the non-breeding season.

Social interactions are believed to have an important influence on microtine population dynamics (Krebs 1979, 1985, Charnov and Finerty 1980, Hestbeck 1982, Taitt and Krebs 1985). The hypothesis of Charnov and Finerty (1980), that kin selection in voles causes population cycles, has attracted much attention from field workers (Kawata 1985, 1990, Boonstra and Hogg 1988, Ylönen et al. 1990) and theoreticians (Warkowska-Dratnal and Stenseth 1985, Stenseth and Łomnicki 1990). Charnov and Finerty's hypothesis assumes that the degree of relatedness is high in sparse populations of voles and that this favours amicable behaviours between related individuals. The degree of kinship is assumed to be inversely related to population density, and individuals living at high density are thought to experience high dispersal rates and low reproductive success as a result of their interactions with unrelated neighbours. Two

experiments aimed at testing the effect of relatedness on the demography of vole populations have been published; the results are contradictory. Boonstra and Hogg (1988) found no effect of relatedness on the demography of enclosed populations of the meadow vole (*Microtus pennsylvanicus*) whereas Ylönen et al. (1990) found a strong effect of relatedness on the demography of the bank vole (*Clethrionomys glareolus*). Juvenile survival in summer was higher in a population of "friends" than of strangers, i.e. better where the animals were highly related. This resulted in a higher rate of increase in the "friends" population.

In a recent review, Kawata (1990) concluded that the assumptions of the Charnov and Finerty hypothesis are inadequate and that the experimental evidence does not support its predictions. Despite this, evolutionary reasoning predicts that under certain conditions relatedness can influence interactions between individuals. There is an increasing body of evidence indicating that familiarity can influence social interactions in small mammals (Ferkin 1988, Barnard and Fitzsimons 1988) and that neighbouring female voles can be closely-related to each other in natural populations (Boonstra et al. 1987, Pugh and Tamarin 1988, Lambin and Krebs in press).

A second hypothesis that has recently attracted much attention (Hansson and Henttonen 1985, 1988, Henttonen et al. 1987) is an extrinsic explanation of population fluctuations of microtines. It suggests that predation by specialist carnivores, mainly least weasels, is sufficient to explain the strongly cyclic pattern of fluctuation of small mammals in Northern Scandinavia. However, the numerical response of predators usually lags behind an increasing vole population (Pearson 1985). It is not clear whether predation only accelerates declines and holds numbers low or is sufficient to drive population fluctuations. Microtine populations from Northern

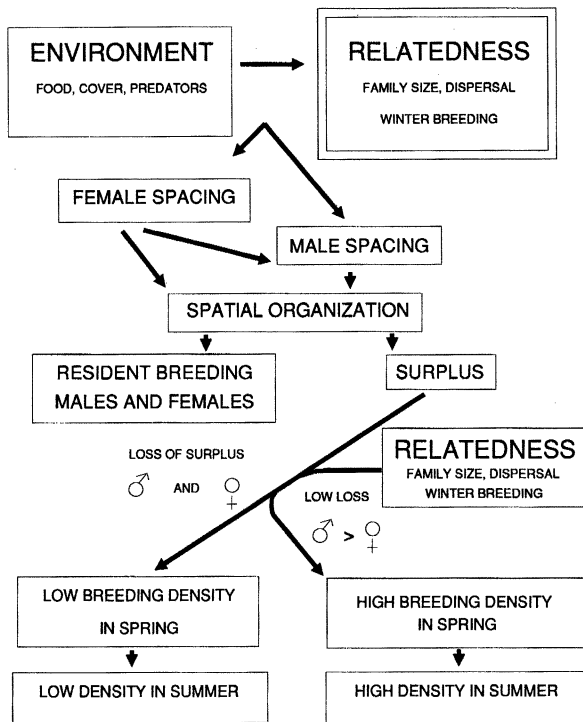


Fig. 1. Cause-effect diagram of the mechanisms postulated to be involved in the population dynamics of microtines indicating how intrinsic and extrinsic factors may interact to influence the degree of relatedness and population dynamics. (Modified from Taitt and Krebs 1985)

Scandinavia are clearly cyclic, whereas some microtines from North America and Europe do not show such regular multi-annual fluctuations (Taitt and Krebs 1985, Hansson and Henttonen 1985). Further, in the non-Scandinavian regions, the same population can fluctuate with a multi-annual periodicity in some years and show inter-seasonal fluctuations only in other years (Krebs 1979, Getz et al. 1987). Non-cyclic populations experience occasional population outbreaks. The processes causing those outbreaks are considered by some North American researchers (Krebs, Chitty pers. comm.) as equivalent to those occurring in peak years of cyclic populations of Scandinavia. If we are to gain better understanding of the processes involved in microtine population fluctuations, the mechanisms that contribute to shaping patterns of fluctuation should be sought and their effect tested.

In this paper, we present a mechanism involving both extrinsic and intrinsic factors that explains differences in the severity of population declines and in the rate of increase of microtine populations. It is an extension of a multi-factorial model proposed and tested by Taitt and Krebs (1981, 1982, 1983, 1985). Taitt et al. (1981) and Taitt and Krebs (1985) suggested that a marked decline in density during spring characterizes non-cyclic microtine populations, whereas little or no spring decline

occurs in populations that show the characteristics described by Krebs and Myers (1974) as being "cyclic". We reiterate here the significance of the spring decline and suggest that seasonal and inter-individual variation in the use of space are important factors influencing population dynamics. We argue that the genetic structure of a population prior to the spring decline might determine the decline's amplitude. We also argue that extrinsic factors such as predation, that affect the pattern of survival and recruitment, are likely to influence the genetic structure of a population and in turn affect spacing behaviour and thus the breeding density.

The model

The model assumes that competition for space and female territoriality are characteristics of the social organization of most microtines at the beginning of the breeding season. At this time of the year, food resources are relatively scarce and only females with a territory gain breeding status. Populations are thus limited by female spacing behaviour. Females that cannot gain a territory for raising their offspring are driven out of the area and disperse in search of breeding territory or are killed by predators. Female aggressiveness peaks in spring when they take up exclusive territories. Thus spacing behaviour and female territoriality contribute to a decline in numbers before the onset of the breeding season in the spring.

We assume that female voles born in spring and summer are philopatric and often breed close to their mother and sisters. At this time, food resources are becoming more abundant than in early spring and females can breed in non-exclusive home ranges or have smaller territories. Philopatric, related females can have overlapping or adjacent home ranges and are socially organized in matrilineal groups. Directly-related females are assumed to recognize each other and behave less aggressively towards each other than towards unrelated females. Thus in summer, vole populations contain clusters of related females and consequently the average degree of relatedness of neighbours is higher than in spring.

The model also assumes that predation and other causes of mortality during the non-breeding season decreases the size of the clusters of related individuals and favours a "dilution" of families by creating opportunities for settlement by immigrant voles. In most years the matrilineal groups are destroyed by winter mortality and the probability of living close to a relative is low after the winter. We then assume that if relatedness is low in late winter, density will drop when breeding starts because unrelated females will take up exclusive territories. If relatedness is high in spring, closely related females are assumed to use communal territories as they need to devote less energy to protecting their

offspring from aggressive, unrelated neighbours, and this permits a higher density of breeding females.

While low relatedness is produced by predation or immigration during winter, high relatedness in spring can be brought about by winter breeding, low predation during the non-breeding period or by the existence of refuges where matrilineal groups are protected from predators. Winter breeding not only produces new recruits but increases the degree of relatedness and restores matrilineal families prior to the onset of spring breeding.

This model predicts that the degree of relatedness, measured as the probability of living close to a direct female parent or sibling will change seasonally and be higher at the end of the breeding season than at the beginning. We also predict that the degree of relatedness will be higher in the spring of an outbreak year (peak year) than in a normal year of lower density (severe spring decline). We predict that any extrinsic factor that disrupts relatedness among females will be amplified through its effects on social behaviour. Conversely, the effect of winter breeding on population dynamics will be amplified through the effect of female philopatry on relatedness and we predict that winter breeding will precede population outbreaks.

Discussion

Competition for space among females and microtine population dynamics

In most microtine species, competition for space between females and female territoriality appear to be a component of the spatial organization (*Clethrionomys* Bujalska 1973, Saitoh 1981, Gilbert et al. 1986, Bondrup-Nielsen 1986; *Microtus arvalis* Frank 1957, Boyce and Boyce 1988; *M. pennsylvanicus* Madison 1980, Boonstra and Rodd 1983; *M. townsendii* Lambin and Krebs in press; *M. breweri* Zwicker 1989; *M. montanus* Jannett 1978; *M. ochrogaster* Getz and Hofmann 1986; *Pitymys* Salvioni 1988). In two species formerly thought to have non-territorial females (*M. agrestis* Myllymäki 1977; *M. californicus* Ostfeld 1986), competition for space between females and female territoriality have been observed at the beginning of the breeding season (Salvioni and Lidicker 1989, Erlinge et al. 1989). Thus in some species females are territorial during the whole breeding season while in other species female territoriality is restricted to the beginning of the breeding season (Lambin and Krebs in press). These observations have led to the suggestion that female spacing behaviour is limiting populations in most microtines (Bujalska 1973, Boonstra and Rodd 1983, Taitt and Krebs 1983). Food addition experiments have induced a decrease in female home ranges (Taitt and Krebs 1983) and an increase in overlap between females' ranges (Ims 1987). This indicates that competition for space be-

tween female voles is affected by the level of food resources.

In outbreak years, female *M. townsendii* do not exhibit any spring decline while males can experience a slight decline or have stable numbers through spring (Taitt and Krebs 1985). Krebs and Boonstra (1978) suggested for this species that spring declines are the result of socially-induced mortality but Taitt and Krebs (1983) demonstrated that predation contributed to the first part of the spring decline, at the onset of the breeding season, while spacing behaviour caused the second part of the decline. Both male and female *M. townsendii* are territorial in spring and competition for space in establishing breeding territories can be equated to spacing behaviour (Lambin and Krebs in press). In contrast to Taitt and Krebs, Erlinge et al. (1983) believe that most disappearing voles from their non-cyclic southern Scandinavian *M. agrestis* populations can be accounted for by predation and they do not believe that social behaviour plays an important role in spring declines.

Taitt and Krebs (1985) have argued that the number of breeding females in spring is closely related to extrinsic factors such as the abundance of food, space and cover. If the spring decline is caused by female territoriality, the absence of such a decline in some years would either indicate a change in spacing behaviour of individuals or a change in the abundance of a limiting resource such as food, allowing more females to establish territories (see Taitt and Krebs 1983, Ims 1987). Here, we argue that *changes in spacing behaviour are caused by changes in the degree of female relatedness.*

Female philopatry and the genetic structure of populations

Recent research has revealed that breeding females of several microtine species show great individual variation in space use (Ims 1989). Even though most female microtines compete for space in spring, pairs of females may share territories and even raise their litters in the same nest at this time (Boonstra and Rodd 1983, McShea and Madison 1984, Taitt, pers. obs. Lambin, pers. obs.). Although genetic relatedness has not been established in most instances, these may be mother-daughter or sister associations and space-sharing between related females could be instances of kin-selection. We have documented cases in which pairs of closely-related females share territories or raise their litters communally in spring while all other females are defending exclusive territories (Lambin unpubl.). If unrelated females compete for exclusive territories during the spring decline and related females share their territories, spring populations composed of related female voles would show a much higher density.

Boonstra et al. (1987) showed that, in four *Microtus* species, about twice as many females as males matured near their natal site, and they suggested that the basic

social organization of females in all species is one based on female kin clusters. Sandell et al. (1990) also found that female *M. agrestis* are more philopatric than males. Female philopatry appears to be the rule among microtines studied to date. While *Clethrionomys* females normally do not reach maturity in the territory of their mothers (Bondrup-Nielsen 1986 but see Gliwicz 1989, Ims 1989), young female *Microtus* can breed in a home range shared with their mothers (Lambin and Krebs in press). Frank (1957) was the first to notice that daughters matured in the maternal home range and he suggested that this feature could allow *M. arvalis* to reach extremely high densities. In other *Microtus* species for which females are territorial at the beginning of the breeding season, small groups of females may share space (Myllymäki 1977, Jannett 1978, McShea and Madison 1984, Heske 1987, Chitty 1987, Lambin and Krebs in press). Furthermore, Boonstra and Rodd (1983) and McShea and Madison (1984) report instances of at least two female meadow voles (*M. pennsylvanicus*) raising their young in the same nest. While philopatric females seem to be tolerated by their mothers and can successfully breed in close proximity to their birth site, very few dispersing females are able to establish themselves in breeding populations (Boonstra and Rodd 1983, Lambin and Krebs in press). Consequently, female kin clusters may be prevalent at the end of the breeding season and the degree of kinship can be high on a small spatial scale (Pugh and Tamarin 1988). Thus the suggestion of Boonstra et al. (1987) that social organization in *Microtus* is based on kin-clusters is supported, but the female kin-clusters are most prevalent at the end of the breeding season.

Effect of mortality and winter breeding on the genetic structure of populations

Clusters of relatives will affect the density of breeding females in the spring if groups of related voles are present in late winter, prior to the breeding season. However, vole populations usually decline through predation during the non-breeding season, and population density is lowest in late winter. Immigration is also more prevalent during the non-breeding season (Krebs et al. 1976), and the probability of an immigrant establishing residency is higher than during the breeding season. Predation in winter thus (1) decreases the size of the clusters of related individuals from the previous breeding season and (2) produces a "dilution" of families by creating opportunities for settlement by immigrant voles. As a result, the probability of living close to a relative should be low in spring of most years and female voles would compete for territories with aggressive unrelated females.

Predation by specialized predators such as weasels *Mustela* spp. could have a very dramatic influence on the degree of relatedness in microtine populations.

Weasels are very efficient predators and they do not move over large distances (Henttonen et al. 1987). Predation can have a direct effect on numbers and an indirect effect on the composition of microtine populations. Intense predation by weasels in some years or continuous predation by generalist predators could prevent the build up of relatedness in some microtine populations. For instance, populations of *M. townsendii* are heavily infested by botflies and grey flesh flies in late summer and autumn (Boonstra 1977, Boonstra et al. 1980) and subject to intense avian predation in winter. Parasites and predators can cause severe mortality and may destroy most matrilineal groups so in most years the degree of relatedness is low by November. The disruption of the genetic structure of Townsend vole populations by parasites in summer might be responsible for the absence of multi-annual fluctuations in populations of this species. Rapid snow melt in spring can also make voles extremely vulnerable to predation and could be responsible for changes in the genetic structure of vole populations.

Winter breeding often occurs in *Microtus* populations prior to outbreaks (Krebs and Myers 1974, Hansson 1984, Keller 1985, Nelson 1987, Krebs in press). In addition to producing new recruits, winter breeding causes new family groups to be formed before spring, thus increasing the degree of relatedness in a given population. Breeding under the snow where small mammals are protected from aerial predators is likely to have dramatic effects on the degree of relatedness. After a winter of breeding under the snow, female neighbours of a breeding female are likely to be direct relatives, as in summer. The "fence effect" observed in some microtine species (Krebs et al. 1969, Boonstra and Krebs 1977) could be interpreted as being a consequence of high relatedness in situations where dispersal is prevented and no immigration is possible (Chitty 1987). High relatedness would induce space-sharing between females and be responsible for the high densities reached by fenced populations.

Consequences of space-sharing among related females

Evidence available to date indicates that familiarity is the basis for kin-recognition in small mammals (Gavish et al. 1984, Ferkin 1988, Barnard and Fitzsimons 1988). It is thus likely that only closely-related females will recognize each other and that only females living in adjacent ranges can maintain recognition in time through their social interactions. It is not known whether unrelated, familiar females also develop preferential relationships and behave like related females in spring. If they do, familiarity relationships would then be more important than genetic relationships in influencing spacing behaviour and the intensity of competition for space between females. Space-sharing by familiar

Table 1. Different assumptions and predictions of the Charnov and Finerty model and the model presented here.

	Charnov and Finerty	Lambin and Krebs
<i>Assumptions:</i>	Kin groups result from low dispersal and inbreeding in low density populations. Relatedness declines in increasing populations because of high dispersal rate. High relatedness induces higher breeding success because of kin-selection.	Kin groups result from philopatry and a lack of immigration. Kin groups disappear because of predation and immigration. High relatedness increases breeding density through reduced competition for space between closely related females in spring.
<i>Predictions:</i>	Average relatedness is higher at low density than at high density. Competition for space is most intense at high density.	The degree of female relatedness fluctuates seasonally. Relatedness increases during the breeding season and decreases in winter. Average relatedness is higher in spring of outbreak or peak years than in other years. Competition for space between females is least intense at high density when average relatedness is high.

females could not be cases of kin-selection. Implicit in Boonstra and Hogg's (1988) attempt to test Charnov and Finerty's hypothesis was the assumption that female voles should recognize relatives even when they are unfamiliar to each other. Indeed, most individuals used to stock their "friends" enclosures were not familiar although closely-related to one another. If voles do not use direct recognition mechanisms to discriminate relatives, the "friends" and the "strangers" populations used by Boonstra and Hogg were only marginally different from each other. This factor alone may explain the striking differences between the results of Ylönen et al. (1990) and Boonstra and Hogg (1988).

Ostfeld (1985) claimed that the renewability of the food resource determined whether or not females can breed within overlapping home ranges. His assertion is not supported since the spacing patterns of breeding female *Microtus* change seasonally from strict territoriality at the beginning of the breeding season to largely overlapping ranges in summer (Lambin and Krebs in press, Salvioni and Lidicker 1989, Erlinge et al. 1989). It is at the beginning of the breeding season, when food resources may be limiting that the existence of groups of related females is more likely to affect spacing patterns and the density of breeding females. If the only function of female territoriality is to secure resources for breeding, females sharing space in spring, related or not, would have to share resources on the defended area. This must set a lower limit to the territory size that related females will tolerate. The potential cost of sharing resources could be compensated for by other advantages accruing from sharing a territory with a kin, such as an increased growth of offspring through cross-lactation (Ayer and Whitsett 1980), an increased survival of offspring through nest-sharing or better thermoregulation for the juveniles (McShea and Madison 1984), and reduced risk of predation and infanticide due to increased attendance at the nest (McShea and Madison 1984) or better ability to acquire an exclusive home range (Kawata 1987) after surviving the time of most severe competition for space. Increased fitness of philo-

patric females, however, is not necessary for space-sharing to induce a high spring female density but it could amplify the demographic consequences of space-sharing.

Conclusion

Charnov and Finerty (1980) suggested that kin selection is the causal mechanism for cyclic fluctuations of small mammal populations. We present a mechanism that can contribute to changes in population density in microtines, but it does not provide a sufficient explanation of population cycles. We still do not know why winter breeding can occur in some years and not in others (Nelson 1987). However, the hypothesis we present can account for the patterns of fluctuation observed in different geographical locations in different years. Unlike Charnov and Finerty, we do not assume that voles are able to recognize their kin without familiarity and we do not invoke the occurrence of inbreeding to cause change in the degree of relatedness. The change in degree of relatedness with density predicted by this model is opposite from that predicted by Charnov and Finerty (Table 1). Charnov and Finerty's model predicts that the degree of relatedness is highest at low density and lowest at high density, whereas we predict that the degree of relatedness, measured as the probability of living close to a direct female parent will change seasonally and be higher at the end of the breeding season than the beginning. We predict that the degree of relatedness will be higher in an outbreak year (little or no spring decline, peak year) than in a normal year of lower density (severe spring decline).

A critical test of the hypothesis presented above, would be to alter the genetic structure of vole populations by manipulating the degree of relatedness or the turnover rate of individuals. The demography and the pattern of space use of resulting populations of different relatedness should be monitored in spring when competition for space between females is most

severe. The size of the clusters of related females living in proximity to each other can be manipulated by selective removal. Ideally, the effect of genetic relationship should be separated from the effect of familiarity, and dispersal should not be prevented by fencing. Dispersal or the lack thereof is the most important factor that influences relatedness in natural populations.

Acknowledgements – This research was supported by the Natural Science and Engineering Research Council of Canada (Grant A6386) to C. J. K. X. L. is a research assistant of the National fund for Scientific Research (Belgium). We thank V. Baucau, D. Chitty, W. Klenner, J. Myers, J. Smith and M. Taitt for stimulating discussion and helpful comments on the manuscript.

References

- Ayer, M. L. and Whitsett, J. M. 1980. Aggressive behaviour of female prairie deer mice in laboratory populations. – *Anim. Behav.* 28: 763–771.
- Barnard C. J. and Fitzsimons J. 1988. Kin recognition and mate choice in mice: the effects of kinship, familiarity and social interference on intersexual interaction. – *Anim. Behav.* 36: 1078–1090.
- Bondrup-Nielsen, S. 1986. Investigation of spacing behaviour of *Clethrionomys gapperi* by experimentation. – *J. Anim. Ecol.* 55: 269–279.
- Boonstra R. 1977. Effect of the parasite *Wohlfahrtia vigil* on *Microtus townsendii* populations. – *Can. J. Zool.* 55: 1057–1060.
- and Hogg, I. 1988. Friends and strangers: a test of the Charnov-Finerty hypothesis. – *Oecologia (Berl.)* 77: 95–100.
- and Krebs, C. J. 1977. A fencing experiment on a high-density population of *Microtus townsendii*. – *Can. J. Zool.* 55: 1166–1175.
- and Rodd, F. H. 1983. Regulation of breeding density in *Microtus pennsylvanicus*. – *J. Anim. Ecol.* 52: 757–780.
- , Krebs, C. J. and Beacham T. 1980. Impact of botfly parasitism on *Microtus townsendii* populations. – *Can. J. Zool.* 58: 1683–1692.
- , Krebs, C. J., Gaines, M. S., Johnson, M. L. and Craine, I. T. M. 1987. Natal philopatry and breeding systems in voles (*Microtus* spp.). – *J. Anim. Ecol.* 56: 655–673.
- Boyce, C. C. K. and Boyce, J. L. III. 1988. Population biology of *Microtus arvalis*. I. Lifetime reproductive success of solitary and grouped breeding females. – *J. Anim. Ecol.* 57: 711–722.
- Bujalska, G. 1973. The role of spacing behaviour among females in the regulation of reproduction in the bank vole. – *J. Reprod. Fertil. Suppl.* 19: 465–474.
- Charnov, E. and Finerty, J. P. 1980. Vole population cycles: a case for kin-selection? – *Oecologia (Berl.)* 45: 1–2.
- Chitty, D. 1987. Social and local environment of the vole *Microtus townsendii*. – *Can. J. Zool.* 65: 2555–2566.
- Erlinge, S., Agrell, J., Nelson, J., and Sandell, M. 1989. Social organization and population dynamics in a field vole (*Microtus agrestis*) population in Southern Sweden. – Abstract of papers and posters. Vol. 1: 78. Fifth International Theriological Congress Rome 1989.
- , Göransson, G., Hansson, L., Högstedt, G., Liberg, O., Nilsson, I. N., Nilsson, T., von Schantz, T. and Sylvén, M. 1983. Predation as a regulating factor on small rodent populations in southern Sweden. – *Oikos* 40: 36–52.
- Ferkin, M. H. 1988. The effect of familiarity on social interactions in meadow voles, *Microtus pennsylvanicus*: a laboratory and field study. – *Anim. Behav.* 36: 1816–1822.
- Frank, F. 1957. The causality of microtine cycles in Germany. – *J. Wildl. Manage.* 21: 113–121.
- Gavish, L., Hofmann, J. E. and Getz, L. L. 1984. Sibling recognition in the prairie vole, *Microtus ochrogaster*. – *Anim. Behav.* 32: 362–366.
- Getz, L. L. and Hofmann, J. E. 1986. Social organization in free-living prairie voles *Microtus ochrogaster*. – *Behav. Ecol. Sociobiol.* 18: 275–282.
- , Hofmann, J. E., Klatt, B. J., Verner, L., Cole, R. F. and Lindroth, R. L. 1987. Fourteen years of population fluctuations of *Microtus ochrogaster* and *M. pennsylvanicus* in east central Illinois. – *Can. J. Zool.* 65: 1317–1325.
- Gilbert, B. S., Krebs, C. J., Talarico, D. and Cichowski, D. B. 1986. Do *Clethrionomys rutilus* females suppress maturation of juvenile females? – *J. Anim. Ecol.* 55: 543–552.
- Gliwicz, J. 1989. Individuals and populations of the bank vole in optimal, suboptimal and insular habitats. – *J. Anim. Ecol.* 58: 237–247.
- Hansson, L. 1984. Winter reproduction in small mammals in relation to food conditions and population dynamics. – *Spec. Pub. Carnegie Mus. Nat. Hist.* 10: 225–234.
- and Henttonen, H. 1985. Gradients in density variation of small rodents: the importance of latitude and snow cover. – *Oecologia (Berl.)* 67: 394–402.
- and Henttonen, H. 1988. Rodent dynamics as community processes. – *Trends Ecol. Evol.* 3: 195–200.
- Henttonen, H., Oksanen, T., Jortikka, A. and Haukialmi, V. 1987. How much do weasels shape microtine cycles in the northern Fennoscandian taiga? – *Oikos* 50: 353–365.
- Heske, E. J. 1987. Spatial structuring and dispersal in a high density population of the California vole, *Microtus californicus*. – *Holarct. Ecol.* 10: 137–148.
- Hestbeck, J. B. 1982. Population regulation of cyclic mammals: the social fence hypothesis. – *Oikos* 39: 157–163.
- Ims, R. A. 1987. Response in spatial organization and behaviour to manipulations of the food resource in the vole *Clethrionomys rufocanus*. – *J. Anim. Ecol.* 56: 585–596.
- 1989. Kinship and origin effects on dispersal and space sharing in *Clethrionomys rufocanus*. – *Ecology* 70: 607–616.
- Jannett, F. J. Jr. 1978. The density-dependent formation of extended maternal families of the montane vole, *Microtus montanus nanus*. – *Behav. Ecol. Sociobiol.* 3: 245–263.
- Kawata, M. 1985. Mating system and reproductive success in a spring population of the red-backed vole, *Clethrionomys rufocanus bedfordiae*. – *Oikos* 45: 181–190.
- 1987. The effect of kinship on spacing among female red-backed voles, *Clethrionomys rufocanus bedfordiae*. – *Oecologia (Berl.)* 72: 115–122.
- 1990. Fluctuating populations and kin interaction in mammals. – *Trends Ecol. Evol.* 5: 17–20.
- Keller, B. L. 1985. Reproductive patterns. – In: Tamarin, R. H. (ed.), *Biology of New World Microtus*. *Am. Soc. Mammal. Spec. Publ.* 8: 725–778.
- Krebs, C. J. 1979. Dispersal, spacing behaviour, and genetics in relation to population fluctuations in the vole *Microtus townsendii*. – *Fortschr. Zool.* 25: 61–77.
- 1985. Do changes in spacing behaviour drive population cycles in small mammals? – In: Sibly, R. M. and Smith, R. H. (eds.), *Behavioural ecology: ecological consequences of adaptive behaviour*. *Symp. Br. Ecol. Soc.* 25: 295–312.
- in press. Are lemmings large *Microtus* or small reindeer? A review of lemming cycles after 25 years and recommendations for future work. – *Biol. J. Linn Soc.* 00: 000–000.
- and Boonstra, R. 1978. Demography of the spring decline in populations of the vole *Microtus townsendii*. – *J. Anim. Ecol.* 47: 1007–1015.
- and Myers, J. H. 1974. Population cycles in small mammals. – *Adv. Ecol. Res.* 8: 267–399.
- , Keller, B. I. and Tamarin, R. H. 1969. *Microtus* population biology: demographic changes in fluctuation populations of *M. ochrogaster* and *M. pennsylvanicus* in southern Indiana. – *Ecology* 50: 587–607.

- , Wingate, I., Leduc, J., Redfield, J. A., Taitt, M. and Hilborn, R. 1976. *Microtus* population biology: dispersal in fluctuating populations of *M. townsendii*. – *Can. J. Zool.* 54: 79–95.
- Lambin, X. and Krebs, C. J. in press. Spatial organization and mating system of *Microtus townsendii*. – *Behav. Ecol. Sociobiol.* 00: 000–000.
- Madison, D. M. 1980. Space use and social structure in meadow voles, *Microtus pennsylvanicus*. – *Behav. Ecol. Sociobiol.* 7: 65–71.
- McShea, W. J. and Madison, D. M. 1984. Communal nesting between reproductively active females in a spring population of *Microtus pennsylvanicus*. – *Can. J. Zool.* 62: 344–346.
- Myllymäki, A. 1977. Intraspecific competition and home range dynamics in the field vole *Microtus agrestis*. – *Oikos* 29: 553–569.
- Nelson, R. J. 1987. Photoperiod-nonresponsive morphs: a possible variable in microtine population-density fluctuations. – *Am. Nat.* 130: 350–369.
- Ostfeld, R. S. 1985. Limiting resources and territoriality in microtine rodents. – *Am. Nat.* 126: 1–15.
- 1986. Territoriality and mating system of California voles. – *J. Anim. Ecol.* 55: 691–706.
- Pearson, O. P. 1985. Predation. – *Spec. Publ. Am. Soc. Mammal.* 8: 535–566.
- Pugh, S. R. and Tamarin, R. H. 1988. Inbreeding in a population of meadow voles, *Microtus pennsylvanicus*. – *Can. J. Zool.* 66: 1831–1834.
- Saitoh, T. 1981. Control of female maturation in high density population of the red-backed vole *Clethrionomys rufocanus bedfordiae*. – *J. Anim. Ecol.* 50: 79–87.
- Salvioni, M. 1988. Home range and social behavior of three species of European *Pitymys* (Mammalia, Rodentia). – *Behav. Ecol. Sociobiol.* 22: 203–210.
- and Lidicker, W. Z. 1989. Seasonal and sexual effects on territoriality in the California vole. – Abstract of papers and posters, Vol. 1: 99. Fifth International Theriological Congress, Rome 1989.
- Sandell M., Agrell, J., Erlinge, S., and Nelson, J. 1990. Natal dispersal in relation to population density and sex ratio in the field vole, *Microtus agrestis*. – *Oecologia (Berl.)* 83: 145–149.
- Stenseth, N. C. and Łomnicki, 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.
- Taitt, M. J. and Krebs, C. J. 1981. The effect of extra food on small rodent populations: II. Voles (*Microtus townsendii*). – *J. Anim. Ecol.* 50: 125–137.
- and Krebs, C. J. 1982. Manipulation of female behaviour in field populations of *Microtus townsendii*. – *J. Anim. Ecol.* 51: 681–690.
- and Krebs, C. J. 1983. Predation, cover, and food manipulations during a spring decline of *Microtus townsendii*. – *J. Anim. Ecol.* 52: 837–848.
- and Krebs, C. J. 1985. Population dynamics and cycles. – *Spec. Publ. Am. Soc. Mammal.* 8: 567–620.
- Gipps, J. H. W., Krebs, C. J. and Dundjerski, Z. 1981. The effect of extra food and cover on declining populations of *Microtus townsendii*. – *Can. J. Zool.* 59: 1593–1599.
- Ylönen, H., Mappes, T. and Viitala, J. 1990. Different demography of friends and strangers: an experiment on the impact of kinship and familiarity in *Clethrionomys glareolus*. – *Oecologia (Berl.)* 83: 333–337.
- Warkowska-Dratnal, H. and Stenseth, N. C. 1985. Dispersal and the microtine cycle: comparison of two hypotheses. – *Oecologia (Berl.)* 65: 468–477.
- Zwicker, K. 1989. Home range and spatial organization of the beach vole, *Microtus breweri*. – *Behav. Ecol. Sociobiol.* 25: 161–170.