

How does rodent behaviour impact on population dynamics?

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Abstract. Rodent social behaviour has been studied extensively but whether or not social behaviour impacts population dynamics has been questioned. Social behaviour is affected by population density and the question is whether or not this is a circular causal system. Infanticide, dispersal, sexual maturation, and direct aggression are all potential processes that are a part of spacing behaviour in rodents. We need to know both the frequency and strength of these processes in rodents, and how they change with population abundance. Recruitment in rodent populations may be limited by the presence of breeding adults, and the kin structure of populations may affect the potential rate of population growth. Survival of neonates in the nest is poorly studied in rodents and very high losses at this stage may prevent population growth in some populations. We need additional experiments to address and uncouple the potential interaction of social behaviour and extrinsic processes like predation in limiting population abundance in natural populations of rodents.

Introduction

Rodents have been a favourite group for both ecological and behavioural studies, and the background of literature now available in these two scientific disciplines would fill a good library (Stoddart 1979; Watts and Aslin 1981; Elwood 1983; Cockburn 1988; Anderson 1989; Prakash and Ghosh 1992; Singleton et al. 1999). Detailed studies of behaviour are available for some species (e.g. Eisenberg 1962, 1963; Gliwicz 1997) and the broad categories of rodent social organisation are well understood. What is lacking is the bridge between rodent social organisation and rodent population dynamics, and this paper reviews the background of this issue and suggests gaps in need of further studies and experiments.

Avian ecologists had already suggested in the 1920s and 1930s that territorial behaviour could limit population density (Howard 1920; Nice 1937; Hensley and Cope 1951). Mammal ecologists were slower to accept that social behaviour might impact population dynamics, and the first approach was through physiology. Hans Selye in 1936 (Selye 1936) suggested that crowding in rodents could lead to physiological stress mediated through the adrenal gland, and stress could reduce reproductive output as well as increase death rates. David E. Davis and John Christian (Davis and Christian 1956) did the first field experiments to show that aggressive social interactions could reduce Norway rat population size, and since these

early experiments, many authors have contributed studies that evaluate the role of social behaviour in affecting population events. In this paper I will examine our current understanding of how social processes might affect rodent population dynamics.

Mechanisms of social limitation

Social behaviour can affect population dynamics via four different mechanisms: control of the timing of sexual maturation, infanticide, control of dispersal, and direct aggression (= interference competition). Wolff (this volume) has reviewed these aspects of the social ecology of rodents and has concluded that social interactions play little role in regulating or stabilising rodent populations. I will not review the detailed aspects of these social interactions, which are covered well in Wolff (this volume) but I wish to concentrate here on his conclusion that social interactions are rarely relevant to population dynamics.

The key behaviours in rodents that might impact on population density can be broadly classed as spacing behaviour. If individual rodents maintain a personal or group space, then clearly the density of that population will reflect this spacing. Spacing is most readily thought of as resulting from direct physical aggression, but this mental image must be broadened to include spacing by avoidance behaviour as well as spacing by direct physical interactions. We first ask if spacing behaviour could limit

population density. Watson and Moss (1970) suggested that limitation might occur if three conditions could be satisfied:

1. a substantial part of the population does not breed ('surplus animals');
2. the non-breeding individuals can breed if the social dominants are removed; and
3. the breeding individuals are not using up some other limiting resource.

Populations that satisfy these three conditions can be considered to be limited by 'social space', and the resource being competed for can be considered to be 'competitor-free space'. Let us consider now how we have tested for these three conditions of Watson and Moss (1970).

Surplus individuals

The first problem in testing for possible population limitation by spacing behaviour has been to determine if 'surplus' animals are present. Following the lead of early experiments on songbirds (Hensley and Cope 1951), rodent ecologists used removal experiments to measure the number of surplus rodents. Krebs (1966) reports one early experiment on *Microtus californicus* in California. These and many other removal experiments have shown that when you remove breeding adult rodents from an area, a flood of 'surplus' individuals colonise the removal site, and in many cases bring the population density of the removal site back to the control density (e.g. Krebs et al. 1978). These removal experiments raise many issues that are relevant to rodent pest control: Where do these 'surplus' animals come from? What is their fate if a removal experiment is not taking place? Do the 'surplus' animals differ in age, sex, or size from resident animals? Many of these questions have been discussed by Anderson (1989) and Cockburn (1988). Clearly, if we accept the standard Darwinian principles, each of these individuals is attempting to maximise its own fitness, and our explanations of these results must fit in with contemporary evolutionary theory. Removal experiments to assess 'surplus' individuals have been criticised in some species, since adjacent territory owners may shift their home ranges into the evacuated area (Schieck and Millar 1987). This criticism will affect the quantitative measurement of 'surplus' animals, but it does not eliminate them. Schieck and Millar (1987) and Clinchy et al. (2001) have shown that 'surplus' animals immigrate into unmanipulated areas as well as local residents shifting their home ranges into the evacuated area.

Given that we have 'surplus' individuals, the second question is whether or not these individuals can breed when given the opportunity. Our results with removal experiments on *Microtus* voles have shown that there is no impediment to breeding in 'surplus' voles, once the residents have been artificially removed from the area (Myers and Krebs 1971; Krebs et al. 1978). The impact of adult females on maturation of juvenile females has been studied particularly well in *Clethrionomys* voles (Bujalska

1970; Gilbert et al. 1986; Kawata 1987). The conclusion to date is that if there are surplus individuals in a rodent population, they are capable of breeding if social controls of maturation are relaxed.

Territoriality

If breeding male or female rodents defend a territory, the potential exists for spacing behaviour to limit population density. The larger a territory that is defended, the lower the population density, and the immediate question arises as to what determines territory size. There has been an ongoing argument in the bird literature between those who interpret territory size as a consequence of population density and those who interpret it as a cause:

territory size → population density

population density → territory size

The only way to test these two views is to experimentally manipulate territory size, typically by manipulating aggression (e.g. Watson and Jenkins 1968), but few of these kinds of experiments have been done on wild rodents (Gipps et al. 1981; Taitt and Krebs 1982) because they are technically difficult.

There is an enormous literature on the behavioural aspects of territoriality, and the question we need to ask here is whether we can treat territorial behaviour as a 'black box' and analyse the population consequences via population-level experiments (a top-down approach), or whether we need a bottom-up approach through detailed ethological studies of territoriality. This question is largely unanswered, and I will proceed under the assumption that we can adopt a top-down approach to understanding territoriality.

Recruitment

A key question in rodent population dynamics is what controls recruitment. Rodents are model systems of species with very high reproductive rates coupled with high death rates, and the question we need to answer is what happens to all the young produced in a rodent population. The general finding in rodent trapping studies is that only a low fraction of the young produced ever recruit into the breeding population (Adler et al. 1987). The assumption is usually made that predators, diseases, bad weather and other environmental factors control the survival of juveniles in their first few weeks of life.

Adult rodents can limit the recruitment of juveniles, and this can be another critical bridge between social behaviour and population dynamics. If adults can limit recruitment of juveniles, we must ask if both sexes are involved or only one. We carried out a series of sex-specific removal experiments on voles that showed conclusively that adult females were, for the most part, the key to understanding why recruitment is restricted. We carried out bi-weekly sex-specific removal experiments on *Microtus townsendii* and *M. oregoni* for two years (Redfield et al. 1978) and the results are illustrated in Figure 1. Recruitment was 109% higher in the area with a more male-biased sex ratio, compared with a control area, and 32% lower in the area with a more female-biased sex

ratio. The same pattern was found in a more carefully controlled experiment with the same basic design with *Microtus canicaudus* by (Wolff et al. 2002). Boonstra (1978) showed with a juvenile introduction experiment that young juvenile *M. townsendii* would survive well if introduced at 3 weeks of age into a field from which all the adults had been removed, but few survived introduction into a field with only adult females present or both adult sexes present (Figure 2). The implication is that adult females directly kill strange juveniles or drive them out of the area, thereby limiting recruitment locally.

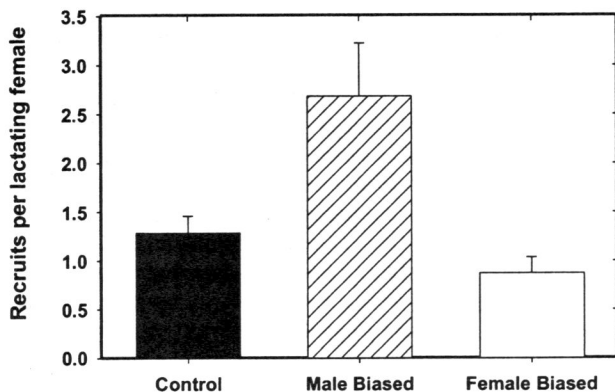


Figure 1. The average recruitment of juvenile *Microtus townsendii* for the summer breeding seasons of 1972 and 1973 on control (unmanipulated), male-biased (80% adult females removed) and female-biased (80% adult males removed) areas. Recruitment was measured as the number of juveniles live-trapped at 2–5 weeks of age per pregnancy. Error bars are 95% confidence limits. (Data from Redfield et al. 1978, Table 6.)

Kinship effects

If spacing behaviour can affect the recruitment rate of young animals, as well as their rate of sexual maturation, we need to find out more information about the rules that govern spacing behaviour in rodents. Darwinian arguments about inclusive fitness would suggest that, for a start, relatives should respond differently to one another than they should to strangers. This simple idea spawns several questions about how relatives might recognise one another, and how familiarity might substitute for genetic relatedness, but the first question we need to answer is whether or not there is a genetic structure of relatives in field populations. Lambin and Krebs (1991) suggested that, since females controlled recruitment in voles, changes in female relatedness might have a significant impact on population dynamics (Figure 3). To test this idea, Lambin and Yoccoz (1998) manipulated the size of matrilineal kinship groups in *M. townsendii* in open populations. Relatives nested closer to one another than did unrelated females, and pup survival in the nest was improved in the first 2 weeks of life when relatives were nearby. In addition, adult female survival at the start of the breeding season was higher for kin group females than for unrelated females. If these kinds of kinship effects are significant, populations with matrilineal will

grow faster than those with only unrelated females, as illustrated schematically in Figure 3. Lambin and Yoccoz (1998) calculated with a simple Leslie matrix model that the differences in juvenile survival alone would change the monthly growth rate (λ) from 1.28 in low kinship groups to 1.43 in high kinship groups. By contrast, Dalton (2000) analysed kin group effects in *M. canicaudus* and found no effects of kin on population growth rates. These kinds of studies need to be done on other rodent species before we will know if kinship effects are quantitatively significant in affecting rates of population growth in natural populations.

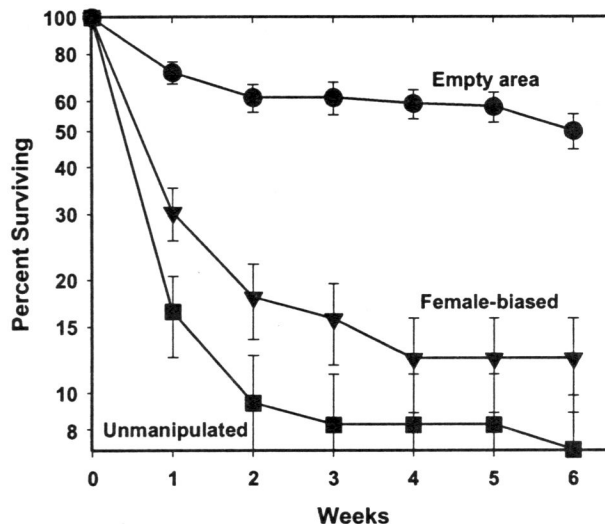


Figure 2. Kaplan-Meier survivorship curves (± 1 se) of juvenile voles (*Microtus townsendii*) introduced in midsummer into three types of areas: an empty grassland from which all adult and sub-adult voles had been removed; an unmanipulated area from which no voles had been removed; and a female-biased area from which all adult male voles had been removed. There is no significant difference between the survivorship curves of the female-biased and unmanipulated treatments. $n = 85$ juveniles in each treatment. (Data from Boonstra 1978.)

Infanticide

Infanticide is without question the most difficult social process to study in natural populations of rodents. If infanticide is the major cause of death of nestlings in rodents, it could be a major driver of population dynamics. I suggest that many rodent pests like the rice-field rat (*Rattus argentiventer*) in Southeast Asia is a pest because it maintains a matrilineal social structure that reduces infanticide to a minor problem.

At the present we do not have a good quantitative analysis of the rate of loss of nestling rodents. I have attempted to do this in a very preliminary way for the house mouse in south-eastern Australia. Figure 4 shows the changes in abundance of house mice in the Murrumbidgee Irrigation Area of New South Wales in recent years. All of the 4 years were similar in having mid- to late-winter declines and summer increases in abundance.

Table 1 attempts to estimate what fraction of neonates reach recruitment age at 2–4 weeks old. Since there are no

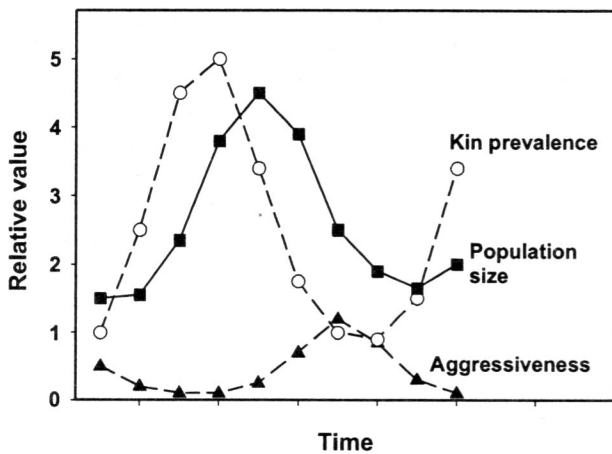


Figure 3. Hypothetical model of the kinship hypothesis of Lambin and Krebs (1991). As the prevalence of kin clusters increases, population density increases with a time lag, with the result of destabilising the dynamics of the population and producing a delayed change in the overall amount of aggression in the population under the general rule that aggression toward kin is low and toward strangers high. This model has been tested by Lambin and Yoccoz (1998) on *Microtus townsendii*.

direct measures of neonate survival, these can only be approximations but the message is still clear: somewhere between 6% and 20% of neonates survive to recruitment in these house mouse populations. Table 1 suggests a possible improvement of neonate survival as the breeding season progresses but this should be considered only a hypothesis that needs direct testing.

For *Microtus* voles, a few estimates of neonate survival are available for comparison. McShea and Madison (1989) found an average survival to recruitment of 31% in *Microtus pennsylvanicus* from 132 litters of radio-collared females. Boonstra and Hogg (1988) by contrast found an average 57% survival of neonates from 43 litters of the same species in an enclosure study. Lambin and Yoccoz (1998) found even higher neonate survival of 70–75% in *M. townsendii*. It is clear that there can be high variability in rodent neonate survival.

What happens to all these neonates? We do not know whether most of these young die in the nest or just after they leave the nest. It seems unlikely that dispersal is a primary cause of loss in the first 3 weeks of life (since dispersal usually occurs at a later age), and there seem to be only three possible agents of loss: predation in the nest, infanticide, and bad weather (e.g. flooding). There are few data available that allow us to partition these causes of loss in any rodent population with the exception of the work of Wolff and Schaubert (1996) on *M. canicaudus* and Lambin and Yoccoz (1998) on *M. townsendii*. Wolff and Schaubert (1996) concluded that infanticide was the cause of reduced juvenile recruitment as adult female density increased. It is clear from a demographic perspective that improvement in the nestling survival rate could presage a large increase in rodent abundance.

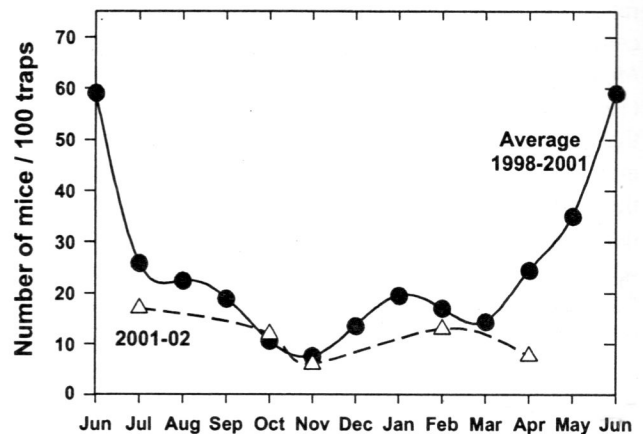


Figure 4. Changes in the abundance of house mice (*Mus domesticus*) in the Murrumbidgee Irrigation Area of New South Wales, Australia, during a series of average years of relatively low abundance. Mice typically decline during the mid- to late-winter months and increase during the summer to reach a peak in the autumn. Two graphs are given for the average density of the years 1998 to 2001 and the 2001–2002 biological year. Cereal and rice-growing areas were the major habitats sampled. (Data courtesy of G.R. Singleton, unpublished.)

Dispersal

If resident adults cause new recruits to disperse, and dispersal is costly in terms of survival in unfamiliar habitats, dispersal could be a process that is involved in population regulation. The most striking experimental argument for the role of dispersal in population regulation has been the fence effect (Krebs et al. 1969; Boonstra and Krebs 1977). The fence effect refers to the observation that rodent populations enclosed in a fence which prevents emigration and immigration reach densities inside the fence that are 5–10 times natural densities and then crash from starvation. Ostfeld (1994) suggested that the fence effect was an artifact of predator exclusion, but this conclusion is incorrect, particularly since Boonstra's site was on an island with no mammalian predators that might be restricted by a fence.

Two general problems have plagued efforts to evaluate the role of dispersal in population limitation. First, dispersal is difficult to measure. Removal areas measure some components of dispersal but may bias the quantitative results (Schieck and Millar 1987). Radio-telemetry studies of dispersal are more promising but sample size problems and scale issues complicate interpretations (Beacham 1980; Gillis and Krebs 1999). Second, if dispersal is to assist in population regulation, it must somehow be related to population density. Many early studies have suggested that dispersal rate is maximum in low density, increasing populations and is minimal at high density (Gaines and McClenaghan 1980).

If this generalisation continues to hold, any dispersal impacts on population regulation or limitation will have to be achieved by indirect means. One way to achieve this

Table 1. Estimates of survival rates of house mouse (*Mus domesticus*) nestlings in the first 3 weeks of life for the years illustrated in Figure 4. Murrumbidgee Irrigation Area, New South Wales, Australia. Litter size is the average over 20 years of data (Singleton et al. 2001). Density estimated from Petersen estimates adjusted with the Davis correction (S. Davis, unpublished). Sex ratio assumed to be 50%. Adult survival rate assumed to be 80% per litter period (20 days). Two estimates of nestling survival are given. The pessimistic estimate utilises the observed proportion of juveniles in the catch each month to estimate juvenile recruitment. The optimistic estimate assumes that half of the population is replaced each month with new recruits. These estimates must be considered as crude approximations to the true survival of nestling mice.

Month	Litter size	Average of 1998–2001 years					2001–2002 year				
		Density of females (per ha)	Output of nestlings	No. recruited	Pessimistic nestling survival (%)	Optimistic nestling survival (%)	Density of females (per ha)	Output of nestlings	No. recruited	Pessimistic nestling survival (%)	Optimistic nestling survival (%)
September	8.50	59	401	16	3.9	14.7	40	275	18	6.6	14.7
October	8.26	33	218	9	4.0	15.1	37	247	17	6.7	15.1
November	8.06	24	152	6	4.1	15.5	19	119	8	6.9	15.5
December	6.52	42	220	11	5.0	19.2	25	129	11	8.5	19.2
January	5.96	61	290	16	5.5	21.0	31	148	14	9.4	21.0
February	4.92	53	209	14	6.7	25.4	40	159	18	11.3	25.4
March	5.16	45	185	12	6.4	24.2	31	128	14	10.8	24.2
April	5.50	77	338	20	6.0	22.7	24	105	11	10.1	22.7
May	5.30	110	466	29	6.2	23.6	31	132	14	10.5	23.6
June	5.00	186	745	49	6.6	25.0	–	–	–	–	–
Totals and weighted averages			3224	181	5.6	19.6		1442	124	8.6	16.5

would be for dispersal to be selective for certain phenotypes that have different types of spacing behaviour (Krebs 1985). Whether or not this occurs in rodents is unclear at present.

Dispersal may have evolved as an inbreeding avoidance mechanism, but the demographic consequences of dispersal may play some role in population limitation, if only by increasing the probability that predators or disease or bad weather will kill dispersing individuals.

Conclusion

There are several mechanisms by which social behaviour can affect birth, death, and dispersal rates and thereby population density changes. In any natural population of rodents, social behaviour will operate in a matrix of extrinsic mechanisms like predation, and disentangling the relative contribution of specific factors can be done only with carefully designed experiments. Given this array of potential impacts, I judge it premature to conclude, as Wolff (this volume) and others have, that social behaviour contributes little to stabilising or regulating rodent population densities. Further experiments will help to decide this issue.

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References

- Adler, G.H., Wilson, M.L. and Derosa, M.J. 1987. Effects of adults on survival and recruitment of *Peromyscus leucopus*. *Canadian Journal of Zoology*, 65, 2519–2544.
- Anderson, P.K. 1989. Dispersal in rodents: a resident fitness hypothesis. *American Society of Mammalogists, Special Publication No. 9*, 142 p.
- Beacham, T.D. 1980. Dispersal during population fluctuations of the vole, *Microtus townsendii*. *Journal of Animal Ecology*, 49, 867–877.
- Boonstra, R. 1978. Effect of adult Townsend voles (*Microtus townsendii*) on survival of young. *Ecology*, 59, 242–248.
- Boonstra, R. and Hogg, I. 1988. Friends and strangers: a test of the Charnov-Finerty hypothesis. *Oecologia*, 77, 95–100.
- Boonstra, R. and Krebs, C.J. 1977. A fencing experiment on a high-density population of *Microtus townsendii*. *Canadian Journal of Zoology*, 55, 1166–1175.
- Bujalska, G. 1970. Reproductive stabilizing elements in an island population of *Clethrionomys glareolus* (Schreber 1780). *Acta Theriologica*, 15, 381–412.
- Clinchy, M., Krebs, C.J. and Jarman, P.J. 2001. Dispersal sinks and handling effects: interpreting the role of immigration in common brushtail possum populations. *Journal of Animal Ecology*, 70, 515–526.
- Cockburn, A. 1988. Social behaviour in fluctuating populations. London, Croom Helm, 239 p.
- Dalton, C.L. 2000. Effects of female kin groups on reproduction and demography in the gray-sided vole, *Microtus canicaudus*. *Oikos*, 90, 153–159.
- Davis, D.E. and Christian, J.J. 1956. Changes in Norway rat populations induced by the introduction of rats. *Journal of Wildlife Management*, 20, 378–383.
- Eisenberg, J.F. 1962. Studies on the behaviour of *Peromyscus maniculatus gambelii* and *Peromyscus californicus parviticus*. *Behaviour*, 19, 177–207.
- Eisenberg, J.F. 1963. The behavior of Heteromyid rodents. University of California Publications in Zoology, 69, 1–114.
- Elwood, R.W. (ed.) 1983. Parental behaviour of rodents. Chichester, Wiley, 296 p.
- Gaines, M.S. and McClenaghan, L.R., Jr. 1980. Dispersal in small mammals. *Annual Review of Ecology and Systematics*, 11, 163–196.
- Gilbert, B.S., Krebs, C.J., Talarico, D. and Cichowski, D.B. 1986. Do *Clethrionomys rutilus* females suppress maturation of juvenile females? *Journal of Animal Ecology*, 55, 543–552.
- Gillis, E.A. and Krebs, C.J. 1999. Natal dispersal of snowshoe hares during a cyclic population increase. *Journal of Mammalogy*, 80, 933–939.
- Gipps, J.H.W., Taitt, M.J., Krebs, C.J. and Dundjerski, Z. 1981. Male aggression and the population dynamics of the vole, *Microtus townsendii*. *Canadian Journal of Zoology*, 59, 147–157.
- Gliwicz, J. 1997. Space use in the root vole: basic patterns and variability. *Ecography*, 20, 383–389.
- Hensley, M.M. and Cope, J.B. 1951. Further data on removal and repopulation of the breeding birds in a spruce–fir forest community. *Auk*, 68, 483–493.
- Howard, H.E. 1920. Territory in bird life. London, Collins, 308 p.
- Kawata, M. 1987. Pregnancy failure and suppression by female–female interaction in enclosed populations of the red-backed vole *Clethrionomys rufocanus bedfordiae*. *Behavioural Ecology and Sociobiology*, 20, 89–97.
- Krebs, C.J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. *Ecological Monographs*, 36, 239–273.
- Krebs, C.J. 1985. Do changes in spacing behaviour drive population cycles in small mammals? In: Sibly, R.M. and Smith, R.H., ed., *Behavioural ecology: ecological consequences of adaptive behaviour*. Oxford, Blackwell, 295–312.
- Krebs, C.J., Keller, B.L. and Tamarin, R.H. 1969. *Microtus* population biology: demographic changes in fluctuating populations of *M. ochrogaster* and *M. pennsylvanicus* in southern Indiana. *Ecology*, 50, 587–607.
- Krebs, C.J., Redfield, J.A. and Taitt, M.J. 1978. A pulsed removal experiment on the vole *Microtus townsendii*. *Canadian Journal of Zoology*, 56, 2253–2262.
- Lambin, X. and Krebs, C.J. 1991. Can changes in female relatedness influence microtine population dynamics? *Oikos*, 61, 126–132.
- Lambin, X. and Yoccoz, N. 1998. The impact of population kinstructure on nestling survival in Townsend's voles, *Microtus townsendii*. *Journal of Animal Ecology*, 67, 1–16.
- McShea, W.J. and Madison, D.M. 1989. Measurements of reproductive traits in a field population of meadow voles. *Journal of Mammalogy*, 70, 132–141.
- Myers, J.H. and Krebs, C.J. 1971. Genetic, behavioral, and reproductive attributes of dispersing field voles, *Microtus pennsylvanicus* and *Microtus ochrogaster*. *Ecological Monographs*, 41, 53–78.

- Nice, M.M. 1937. Studies in the life history of the song sparrow. I. Transactions of the Linnean Society of New York, 4, 1–247.
- Ostfeld, R.S. 1994. The fence effect reconsidered. *Oikos*, 70, 340–348.
- Prakash, I. and Ghosh, P.K. 1992. Rodents in Indian agriculture, 1. Jodhpur, India, Scientific Publishers, 692 p.
- Redfield, J.A., Taitt, M.J. and Krebs, C.J. 1978. Experimental alteration of sex ratios in population of *Microtus townsendii*, a field vole. *Canadian Journal of Zoology*, 56, 17–27.
- Schieck, J.O. and Millar, J.S. 1987. Can removal areas be used to assess dispersal of red-backed voles? *Canadian Journal of Zoology*, 65, 2575–2578.
- Selye, H. 1936. Syndrome produced by diverse nocuous agents. *Nature*, 138, 32.
- Singleton, G.R., Hinds, L., Leirs, H. and Zhang, Z. 1999. Ecologically-based management of rodent pests. ACIAR Monograph No. 59. Canberra, Australian Centre for International Agricultural Research (ACIAR), 494 p.
- Singleton, G.R., Krebs, C.J., Davis, S., Chambers, L. and Brown, P. 2001. Reproductive changes in fluctuating house mouse populations in southeastern Australia. *Proceedings of the Royal Society of London, Series B*, 268, 1741–1748.
- Stoddart, D.M. (ed.) 1979. *Ecology of small mammals*. London, Chapman and Hall, 386 p.
- Taitt, M.J. and Krebs, C.J. 1982. Manipulation of female behaviour in field populations of *Microtus townsendii*. *Journal of Animal Ecology*, 51, 681–690.
- Watson, A. and Jenkins, D. 1968. Experiments on population control by territorial behaviour in red grouse. *Journal of Animal Ecology*, 37, 595–614.
- Watson, A. and Moss, R. 1970. Dominance, spacing behavior and aggression in relation to population limitation in vertebrates. In: Watson, A., ed., *Animal populations in relation to their food resources*. Oxford, Blackwell, 167–220.
- Watts, C.H.S. and Aslin, H.J. 1981. *The rodents of Australia*. London, Angus and Robertson, 321 p.
- Wolff, J.O., Edge, W.D. and Wang, G. 2002. Effects of adult sex ratios on recruitment of juvenile gray-tailed voles, *Microtus canicaudus*. *Journal of Mammalogy* (in press).
- Wolff, J.O. and Schaubert, E.M. 1996. Space use and juvenile recruitment in gray-tailed voles in response to intruder pressure and food abundance. *Acta Theriologica*, 41, 35–43.