Hedmark University College

Faculty of applied ecology and agriculture

BRAGE

Hedmark University College's Open Research Archive

http://brage.bibsys.no/hhe/

This is the author's version of the article published in

Oikos

The article has been peer-reviewed, but does not include the publisher's layout, page numbers and proof-corrections

New views on how population-intrinsic and community-extrinsic processes interact during the vole population cycles

Harry P. Andreassen, Petter Glorvigen, Alice Rémy and Rolf A. Ims

H.P. Andreassen (harry.andreassen@hihm.no), P.Glorvigen (petter.glorvigen@hihm.no), A. Rémy (alice_remy@hotmail.fr), Faculty of Applied Ecology and Agricultural Sciences, Campus Evenstad, Hedmark Univ. College, , No-2480 Koppang, Norway. Fax: +47 62430851. – R.A. Ims (rolf.ims@uit.no), Department of Arctic and Marine Biology, Univ. of Tromsø, No-9037 Tromsø, Norway. Fax: +47 77646020

Corresponding author:
Harry P. Andreassen,
Hedmark University College, Faculty of Applied Ecology and Agricultural Sciences,
Campus Evenstad,
No-2480 Koppang, Norway
Tel: + 47 62430852 / + 47 92832102
Fax: + 47 62430851
E-mail: harry.andreassen@hihm.no

Based on evidence from a series of recent studies linking behaviour to demography in experimental vole populations we propose how extrinsic and intrinsic factors interact through the various phases of the multi-annual population cycles of voles and lemmings. We hypothesise that population growth in the increase phase of the cycle is enhanced by a high degree of space sharing (sociality) among reproductive females who share resource patches, especially during winter. These social females enjoy a high reproductive output due to good resource conditions, and facilitation provided by communal thermoregulation, breeding and defence of weanlings towards infanticidal conspecifics. We hypothesise on the other hand that the crash phase is initiated and enhanced by predation of adult males that leads to a series of cascading events involving infanticidal behaviour by immigrant males, increased mortality of adult social females, and inversely density-dependent and/or disturbance-induced dispersal. These events further enhance predation induced mortality and thus a negative feed-back loop to the rate of the crash. In this framework we may explain how extrinsic factors such as predation and winter resource distribution contribute to transitions between docile and aggressive behaviours, and how this transition is spatially synchronised by inversely density-dependent dispersal that may act to mediate a rapidly spreading wave throughout the population. We propose that innate differences among rodent species in their propensities for different social organizations also determine their propensity for exhibiting multi-annual cycles as well as other cycle-related phenomena such as shape of the population cycles and spatial synchrony. We provide a set of testable predictions for further empirical evaluation.

Introduction

To suggest that both population-intrinsic processes

and community-level processes are essential

for generating periodic fluctuations in rodents, is not new. ...

However, the empirical support for such a synthetic view

has not yet been put together (Stenseth et al. 1996)

Multiannual population cycles are common in small mammals in the Northern hemisphere (Steen et al. 1990, Kendall et al. 1998) and have triggered the interest of population ecologists since Elton (1924, 1942) described this phenomena based on historical data in North-West Europe and Canada (see Lindstrøm et al. 2001). During the last decades predation has received ample support as a driver of rodent cycles, and predation has become accepted as a sufficient driving mechanism for generating vole- and lemming cycles (Stenseth and Ims 1993, Hanski et al. 2001, Turchin and Hanski 2001, Gilg et al. 2003, Turchin 2003, Korpimaki et al. 2004). However, it has been repeatedly confirmed by experiments (Gilbert and Krebs 1981, Batzli 1986, Huitu et al. 2003, Nie and Liu 2005) and in observations of natural populations (Laine and Henttonen 1983, Krebs et al. 2010, Boonstra and Krebs 2012) that small rodent populations also respond to food quality or quantity. Hence, interaction with food plants may contribute to vole cycles (Batzli 1983, Boutin 1990), or even drive small rodent cycles as it has been suggested for lemmings (Turchin et al. 2000, Turchin and Batzli 2001, Oksanen et al. 2008).

In addition to the above mentioned community-level processes (predation and food) various intrinsic factors have also been suggested as cycle generating mechanisms. Maternal effects may in theory be able to create cycles (Ginzburg and Taneyhill 1994, Inchausti and

Ginzburg 1998), while it has been harder to confirm (by modelling) that other mechanisms related to behavioural, physiological or genetic changes in the individuals can generate cycles (Christian 1950, Chitty 1960, 1967, Krebs and Myers 1974, Krebs 1978, 1979, Charnov and Finerty 1980, Christian 1980, Charnov 1981, Boonstra and Boag 1987, Lambin and Krebs 1991, Boonstra and Boag 1992, Lambin et al. 1992, Boonstra 1994, Chitty 1996, Krebs 1996, Boonstra and Hochachka 1997, Tkadlec and Zejda 1998b, a, see also Mougeot et al. 2003, Sutherland et al. 2005 for intrinsic population regulation in grouse and mice populations). However, the behavioural hypothesis by Charnov and Finerty (1980) have gained continued attention as mathematical models showed that it is plausible (Warkowska-Dratna and Stenseth 1985, Matthiopoulos et al. 1998, 2000, 2002, 2003, but see Krebs 1996). Charnov and Finerty (1980) suggested that kin selection drove behavioural changes through the different phases of the population cycle; docile animals organized in kin groups during the increase phase turned aggressive in the peak due to encounters with an increasing number of unrelated dispersing individuals which ultimately caused the population to crash. The modelling study of Stenseth and Lomnicki (1990) did, however, show that the transition between behaviours (docile and aggressive) had to be synchronized to create cycles. While a distinct wave of unfamiliar immigrants could explain the synchronisation from docile to aggressive behaviour, the existence of such a wave or other mechanisms synchronising the transition from aggressive to docile has never been empirically demonstrated.

Charnov and Finerty (1980) suggested that reduced relatedness resulted from increasing dispersal rates. In a related hypothesis Lambin and Krebs (1991) suggested that kin groups were formed by philopatry, and dissolved because of predation and immigration. Charnov and Finerty (1980) predicted that relatedness would be higher at low densities, while Lambin and Krebs (1991) predicted that relatedness should fluctuate seasonally and multi-annually and be highest during the breeding season of outbreak years. Matthiopoulos et al. (1998) verified by

a mathematical model that such kin-structured dynamics easily produced population density cycles.

Most hypotheses developed to describe vole multiannual population cycles are based on single factors (see also Batzli 1992, Stenseth and Ims 1993, Krebs 1996). There have been fewer attempts to consider how the combined action of intrinsic and extrinsic factors may be involved in the generation of population cycles to shape small rodent population dynamics (Bondrup-Nielsen and Ims 1988a, b, Lidicker 1988, Heske and Bondrup-Nielsen 1990, Hansson 1998, see also New et al. 2009 and Krebs 2011 for multi-factorial explanations of grouse and hare cycles). Here we provide an updated view on how intrinsic and extrinsic mechanisms may interact to shape small rodent population dynamics with a focus on multiannual cycles. Our point of departure are empirical results from a series of recent studies conducted on experimental populations of voles (Ims and Andreassen 2000, Andreassen and Ims 2001, Gundersen et al. 2001, Ims and Andreassen 2005, Andreassen and Gundersen 2006, Rémy 2011, Glorvigen et al. 2012a, b). We are not advocating that such interactions are necessary for cyclic population dynamics to emerge. Our aim is rather to elucidate how they may contribute to explain why some species may be more prone to show cycles than others, and moreover, how such behavioural mechanisms may contribute to explain other phenomena connected to population cycles in rodents .We conclude this paper by providing a set of testable predictions for further empirical evaluation of our view on the role of social behaviour and dispersal in multiannual rodent cycles.

Critical phase-dependencies of the rodent cycle

In the experimental studies, forming the empirical basis for this paper, we have been able to link social behaviour and dispersal to demographic responses at time scales and settings that are relevant for the different phases of the rodent cycle.

Increase phase

The increase is initiated from local demes that have survived the bottleneck of the cycle; i.e. the winter of the cycle low phase. Such demes are supposedly located in high quality habitats that are patchily distributed in the landscape (Sundell et al. 2012). The extent of this patchiness is determined by species-specific habitat preferences (e.g. set by the availability of preferred food plants and predation risk), but may be significantly modified by snow conditions in winter (Aars and Ims 2002). This patchy nature of low - early increase phase (meta)populations is emphasised in many models of cyclic vole populations (Lidicker 1973, Stenseth 1978, Charnov and Finerty 1980, Warkowska-Dratna and Stenseth 1985, Stenseth and Lomnicki 1990). Based on recent results of bank voles *Myodes glareolus* (Rémy 2011) we suggest that resource patchiness initiates group formation of social females that have a higher reproductive success than solitary territorial females during increase phase winters (Figure 1). These results stem from enclosed populations of bank voles consisting of 2-5 reproducing females during winter (November – April). We estimated the sociality of the population as the proportion of traps used by females that was used by more than one female. Predictions from regression models show that during winter each female in populations where 2/3 of the traps are used by multiple females will produce twice as many recruits (5.1 recruits per females; Lambda = 1.5) compared to females living in populations where females are completely territorial (i.e. no traps are used by more than one female; 2.4 recruits per females; Lambda = 0.6)). We see the same effect in spring (April – June) when the populations have obtained 4-12 reproducing females; That is: 5.6 recruits per female (Lambda = 2.2) in populations where 67% of the traps are used by multiple females and 4.8 recruits per females (Lambda 2.2) in strictly territorial populations (see Rémy 2011).

Also a number of previous studies have generally verified that sociality at least under certain conditions may enhance reproductive success (Ims 1987a, Ylonen et al. 1990, Ylonen and Viitala 1991, Lambin and Yoccoz 1998, Sutherland et al. 2005). Clumping of individuals and sociality due to resource patchiness may be particularly enhanced during the winter season due to spatially heterogeneous snow conditions (Aars and Ims 2002, Korslund and Steen 2006, Reid et al. 2012). Indeed, the winters are likely to be critical since winter population growth is characteristic of the increase phase of those rodent populations with most profound high amplitude population cycles (Kausrud et al. 2008, Ims et al. 2011).

Given the relatively small group sizes in this phase of the cycle the benefit of group living may outpace the costs in terms of competition for food. The benefits may include communal thermoregulation in winter (Hayes 2000, Gilbert et al. 2010), communal breeding (Andreassen et al. 1990, Hayes 2000), and/or shared protection against infanticide (Wolff 1993, Ylonen et al. 1997, Agrell et al. 1998, Wolff and Peterson 1998).

Based on evidence from our recent studies of experimental root vole *Microtus oeconomus* populations we expect that the dispersal rate will be high during the increase phase. This is due to generally low densities (i.e. inversely density-dependent dispersal) and high spatial variation in densities (Andreassen and Ims 2001). In this phase of the cycle, with a lot of vacant habitat, dispersal leads to colonization of previously empty habitat patches rather than intrusion of immigrants into established social groups. The large capacity of voles for rapid colonisation through a high mobility and active search for vacant patches has recently been demonstrated experimentally by Glorvigen et al. (2012b). New groups of reproductively active colonizers will soon form social fences inhibiting further immigration (Hestbeck 1982, Gundersen et al. 2001). Social female groups with continuous high reproductive output (Rémy 2011) will tend to grow due to philopatry of *in situ* recruited kin, and relatedness will increase towards the peak, in accordance with Lambin and Krebs (1991).

Peak phase

Towards the peak phase of a cycle a declining proportion of animals disperse as dispersal is inversely density dependent (Andreassen and Ims 2001, Lin and Batzli 2001, Lucia et al. 2008). At least partly this inverse density dependence is due to immigration becoming limited by social fences (Hestbeck 1982, Gundersen et al. 2001) as the landscape is getting colonized and "filled up" (e.g. Bondrup-Nielsen and Ims 1988a, see also Glorvigen et al. 2012a). Young animals remain philopatric and become reproductively suppressed due to lack of breeding space (see e.g. Wolff 1997) or density-dependent competition for food. The survival rate may still be high as dispersal rate (risky movements) is low and/or predation pressure is still low.

Crash phase

We suggest that the crash phase of vole population cycles is initiated by increased predation rate resulting from predator numerical and functional responses (e.g. Sundell 2006). Our experimental studies on root voles have demonstrated how the effect of predation may be dramatically enhanced due to an interaction with behavioural mechanisms of this species. In particular, removal of dominant males from social groups due to predation, is subsequently followed by a cascade of detrimental events that leads to a disrupted social system with severe demographic effects (Andreassen and Ims 2001, Andreassen et al. 2002, Andreassen and Gundersen 2006). The effect of losing a dominant male reduces the population growth rate of experimental root vole populations from 1.54 to 0.80 (Andreassen and Gundersen 2006).

Dominant adult males constitute the demographic segment of the population most vulnerable to predation as they roam over large areas and perform risky movements in defence of a group of females, or to gain access to other females in oestrus (Tast 1966, Ims 1988, Lambin et al. 1992, Gliwicz 1997, Andreassen et al. 1998, Haapakoski and Ylonen

2010). Indeed, it is observed that predation-induced turnover in voles is higher in males than in females (Korpimaki 1985, Halle 1988, Mappes et al. 1993). The detrimental cascade initiated by the predation of a dominant male have the following steps: 1) The loss of territorial males will induce influx of immigrating males that appropriate the vacant territory (see Andreassen and Gundersen 2006). 2) The immigrant males will give reduced recruitment due to infanticide (Andreassen and Gundersen 2006, Korpela et al. 2011, Opperbeck et al. 2012). 3) Females that lose their nestlings tend to start risky movements and will be exposed to increased predation (Andreassen and Ims 2001, Stockley and Bro-Jørgensen 2011); and 4) the initially most social and aggregated adult females suffer from the highest mortality following the loss of the dominant male (Andreassen and Gundersen 2006). The effects of reduced reproductive success and increased mortality of female deme members following the turnover of males is by itself sufficient to yield a negative growth of the deme (Andreassen and Gundersen 2006). Note however that negative population growth may be further enhanced by inversely density dependent dispersal (Andreassen and Ims 2001) when combined with the generally high predation pressure in the crash phase (Ims and Andreassen 2000).

The low phase

Little is known about the low phase due to the problems of finding animals to study. We expect however, based on our experimental studies, that inverse density-dependent dispersal is prominent also in this phase of the cycle with a high proportion of individuals dispersing in attempts to colonize newly vacant high quality habitat. However, early in the low phase dispersers are likely to be highly vulnerable to predators, which still will be numerous (Hansson 1984, Reid et al. 1995, Korpimaki and Norrdahl 1998). One may argue that dispersal should not be adaptive under very high predation pressures and that dispersal should

not only be density-dependent but also be predation rate dependent (i.e. phase-dependent).
Our experimental evidence on root vole shows, however, that the dispersal rate appear to be
high even when the experimental populations were subject to exceptional high predation rates
(Ims and Andreassen 2000). It may be that dispersal under such circumstance is a strategy to
escape "spatial predator pits". Still prediction on the behaviour of low-phase animals will be
speculative as there are virtually no studies of small rodents in this phase of the cycle.

Implications and predictions

Our view on how behaviour affects demography during the different phases of the
population cycle dynamics share some premises of the hypotheses by Charnov and Finerty
(1980) and Lambin and Krebs (1991). This regards in particular the important role of the
social organization consisting of female social (kin) groups with a high reproductive output in
the increase phase of the cycle. Here, however, we emphasise this social organization's dual
effect, i.e. that it acts to enhance population growth in the increase phase of the cycle, but also
that it may lead to an opposite demography in the crash phase. In the crash phase, female
social groups defended by territorial males are vulnerable to the impact of an external factor
(predation) that may lead to the chain of detrimental events that enhances population decline.
Our proposal also provides a mechanism for the synchronization of the transition between
docile and aggressive behaviours needed for the Charnov-Finerty (1980) hypothesis to
produce multiannual population cycles (Stenseth and Lomnicki 1990 see also Warkowska-
Dratna and Stenseth 1985). The key here may be synchronization from docile to aggressive
behaviours caused by a spreading wave of immigrants (induced by predation) that disrupts the
social system throughout the population (see also Rémy 2011), and the synchronization from
aggressive to docile induced by winter conditions forcing increased sociality and a rapid
colonisation at low densities.

We also emphasise the important role of dispersal in all phases of the cycle. A relatively new insight provided by our experimental studies is that dispersal is inversely density-dependent. Similar to what we propose in the case of social organization (see above), dispersal may also have opposite demographic effects in the increase and crash phase of the cycle. At low density in the increase phase the high proportion of dispersing animals gives a rapid colonization of vacant habitat patches, which contributes to rapid population growth. At this stage the cost of dispersal is likely to be low (as the density of predators is low) and even long-distance dispersal events across hostile matrix habitat is likely to end up in successful colonization of vacant patches (Glorvigen et al. 2012b, c). While dispersal is halted towards the peak phase, it is found to increase again under the declining population densities of crashing populations (Ims and Andreassen 2000, Andreassen and Ims 2001). As dispersal during the crash phase of the cycle takes place in an environment with a high density of predators, the mortality rate of dispersers is high which thus contributes further to the decline of the population (Ims and Andreassen 2000, Andreassen and Ims 2001). It is presently an emergent view that inversely density-dependent dispersal is the rule for many species (Wiklund 1996, Støen et al. 2006, Loe et al. 2009 see also review in Lambin et al. 2001, Le Galliard et al. 2012), but yet its significance for population dynamics has so far received little attention (but see Ims and Andreassen 2005, Smith et al. 2008).

The way we think intrinsic mechanisms contribute to shaping population dynamics may even be applicable to species that do not have regular population cycles, but rather exhibit population outbreaks at irregular intervals. For instance, the significance of female kin groups in the increase phase has also been proposed for the house mouse *Mus musculus* outbreaks in Australia (Krebs et al. 1995, Sutherland et al. 2005). Female sociality and its role in increasing populations has been demonstrated for several species (e.g. Lambin and Krebs 1993, Rémy 2011), while the role of male turnover in enhancing the population decline of

crashing populations has only been studied in experimental root vole populations (e.g. Andreassen and Gundersen 2006). It is therefore a need for more studies to verify our proposal regarding the role of social behaviour in the crash phase of the rodent cycle. In particular we encourage studies on species with different innate propensities for female social behaviour and male territoriality (e.g. comparing *Myodes*, *Microtus* and lemming spp.). A recent experimental study shows that male turnover also affects bank vole populations negatively (Opperbeck et al. 2012), but only at low densities.

Note that we do not claim that intrinsic mechanisms neither alone nor in interactions with extrinsic factors are necessary for generating multiannual cycles. Indeed, given the present empirical and theoretical evidence there is ample evidence that extrinsic factors (and perhaps most likely predation) are the key drivers of population density cycles. Actually the intrinsic mechanisms described here are responses to extrinsic factors and are therefore not expected to enter into force without the extrinsic trigger. Still we will argue that it is likely that intrinsic factors contribute to shaping rodent populations dynamics (cf. Stenseth et al. 1996) and by taking this into consideration we may be better able to explain why the prevalence of population cycles and associated phenomena vary in time and space. The relative strong effects found on the population growth rate due to sociality and the detrimental effects of male turnover contribute to the abrupt increase and decrease observed in cyclic populations.

Specifically, we propose that innate propensities for different social organization among rodents may predict which species are most prone to exhibit population cycles. In our view population cycles should be most prevalent in species that are socially organized in terms of male territoriality and female social groups. As this type of social organization is more typical to *Microtus* than to *Myodes* (Ostfeld 1985, Ims 1987b) one could expect that cycles are most prevalent in *Microtus* spp. This difference in social organisation may also explain why Opperbeck et al. (2012) found effects of male turnover only at low densities. At low densities

also male bank voles may be functionally territorial due to low densities. At higher densities, the large number of overlapping males and multiple paternity may limit the number of infanticidal males. We are aware of the fact that multi-species rodent communities composed by species with different social organizations exhibit community-wide cycles (e.g. Hansson and Henttonen 1985, Hansen et al. 1999). In that case it may be that the most cycle-prone species is driving the community dynamics (cf. Henttonen 1987 for a similar view).

Our proposal also provides a framework for an alternative understanding of other phenomena associated with population cycles. One such phenomenon is the shape of the cycles which vary tremendously between species (Turchin et al. 2000, Oksanen et al. 2008, Ims et al. 2011). Specifically, it appears to be a contrast in this respect between *Myodes* and *Lemmus* (Ims et al. 2011). *Myodes* populations appear to have lower rates of change both in the increase and the crash phase of the cycle yielding cycles with round (blunt) peaks. In contrast *Lemmus* populations have more abrupt changes in both phases giving sharper (more angular, saw-toothed) cycles. According to the prevailing views these differences are due either to the prevalence of different trophic interactions (predator-prey in *Myodes* and plant-herbivore in *Lemmus*; Turchin et al. 2000, Oksanen et al. 2008) or winter breeding (most prevalent in *Lemmus*; Ims et al. 2011). Here we suggest that innate propensities for different social organizations between the species/genera may be linked to the shape of cycles. Specifically we expect that sharp cycles are typical to species with male territoriality and female sociality. Thus we predict that *Microtus* tends to have sharper cycles than *Myodes*. To our knowledge such a comparison between the two genera has not yet been done. The social system of lemmings is less well known than for the two vole genera. We note however, that it has been described as flexible (Heske and Jensen 1993). Moreover the extreme shifts in dispersal and social behaviour observed in *Lemmus* (in particular in the Norwegian lemming

L. lemmus; Stenseth and Ims 1993) fits well with our proposal that the shape of the cycle may be linked to behaviour and social organization.

Finally, a high degree of spatial synchrony in population dynamics is typical in cyclic rodent populations (Bjørnstad et al. 1999). We expect that the mechanisms that we here propose (i.e. socialisation during winter, high dispersal rates at low densities, and disruption of the social systems by predation) may cause a synchronous transition in behaviours (see above) that also contribute to enhancing spatially synchronous population cycles or rapid travelling waves (Lambin et al. 1998). According to the same line of arguments as expressed above we may predict a link between social system and degree of population synchrony.

To conclude we summarize the set of specific predictions that can be derived from our proposed framework (see Figure 1). We claim that they are all testable by means of experiments or comparative studies on natural populations. While some of them already have received empirical support (as reviewed above) they still need to be tested on more species and in other settings. In particular we stress the need for conducting experiments that are more long-term and invoke a more realistic set of extrinsic factors than the recent experimental studies which have formed the empirical basis for our predictions.

- Environments with high spatial heterogeneity in resources, in particular during harsh winters, create populations with highly social females.

- In the absence of predation, the degree of sociality in females is positively correlated with population growth.

- In the presence of significant predation, sociality in females and male territoriality enhances negative population growth and steep population crashes. Especially crashes taking place during the breeding season ("summer declines") is predicted to be most prevalent in species with such a spacing system.

- During the crash phase the population is characterised by an increasing proportion of adult, aggressive animals and a declining proportion of young animals as recruitment is low due to infanticide. Dispersing animals are highly exposed to predation and show high mortality rate. The adult population is female biased due to high predation rates in adult males.

- Species with a high propensity for flexibility in social behaviour and generally high dispersal rate/range is likely to exhibit cycles with higher amplitude and sharper peaks than less flexible species.

- Species with a highest propensity for flexibility in social behaviour and a dispersal-driven behavioural syndrome is likely to exhibit a greater extent of spatial synchrony in their cycles.

Acknowledgements

References

Aars, J. and Ims, R. A. 2002. Intrinsic and climatic determinants of population demography: the winter dynamics of tundra voles. – Ecology 83: 3449–3456.

Agrell, J. et al. 1998. Counter-strategies to infanticide in mammals: costs and consequences. – Oikos 83: 507–517.

Andreassen, H. P. and Ims, R. A. 2001. Dispersal in patchy vole populations: Role of patch configuration, density dependence, and demography. – Ecology 82: 2911–2926.

Andreassen, H. P. and Gundersen, G. 2006. Male turnover reduces population growth: An enclosure experiment on voles. – Ecology 87: 88–94.

Andreassen, H. P. et al. 1990. A case of communal breeding in the root vole *Microtus oeconomus*. – Fauna 43: 71–73.

Andreassen, H. P. et al. 1998. Space use responses to habitat fragmentation and connectivity in the root vole *Microtus oeconomus*. – Ecology 79: 1223–1235.

Andreassen, H. P. et al. 2002. Dispersal behaviour and population dynamics of vertebrates. – In: Bullock, J. M., Kenward, R. E., and Hails, R. S. (eds.), Dispersal ecology. Cambridge Univ. Press, pp. 237–256.

Batzli, G. O. 1983. Responses of arctic rodent populations to nutritional factors. – Oikos 40: 396–406.

Batzli, G. O. 1986. Nutritional ecology of the California vole - effects of food qualtiy on reproduction. – Ecology 67: 406–412.

Batzli, G. O. 1992. Dynamics of small mammal populations: a review. – In: McCullough, D. R. and Barret, R. H. (eds.), Wildlife 2001: populations. Elsevier Applied Science, pp. 831–850.

Bjørnstad, O. N. et al. 1999. Spatial population dynamics: analyzing patterns and processes of population synchrony. – Trends Ecol. Evol. 14: 427–432.

Bondrup-Nielsen, S. and Ims, R. A. 1988a. Predicting stable and cyclic populations of *Clethrionomys*. – Oikos 52: 178–185.

Bondrup-Nielsen, S. and Ims, R. A. 1988b. Demography during a population crash of the wood lemming, *Myopus-schisticolor*. – Can. J. Zool. 66: 2442–2448.

Boonstra, R. 1994. Population-cycles in microtines - the senescence hypothesis. – Evol. Ecol. 8: 196–219.

Boonstra, R. and Boag, P. T. 1987. A test of the Chitty hypothesis - inheritance of life-history traits in meadow voles *Microtus-pennsylvanicus*. – Evolution 41: 929–947.

Boonstra, R. and Boag, P. T. 1992. Spring declines in *Microtus-pennsylvanicus* and the role of steroid-hormones. – J. Anim. Ecol. 61: 339–352.

Boonstra, R. and Hochachka, W. M. 1997. Maternal effects and additive genetic inheritance in the collared lemming *Dicrostonyx groenlandicus*. – Evol. Ecol. 11: 169–182.

Boonstra, R. and Krebs, C. J. 2012. Population dynamics of red-backed voles (*Myodes*) in North America. – Oecologia 168: 601–620.

Boutin, S. 1990. Food supplemantation experiments with terrestrial vertebrates - patterns, problems, and the future. – Can. J. Zool. 68: 203–220.

Charnov, E. L. 1981. Vole population-cycles - ultimate or proximate explanation. – Oecologia 48: 132–132.

Charnov, E. L. and Finerty, J. P. 1980. Vole population-cycles - a case for kin-selection. – Oecologia 45: 1–2.

Chitty, D. 1960. Population processes in the vole and the relevance to general theory. – Can. J. Zool. 38: 99–113.

Chitty, D. 1967. The natural selection of self-regulatory behaviour in animal populations. – Proc. Ecol. Soc. Aust. 2: 51–78.

Chitty, D. 1996. Do lemmings commit suicide? Beautiful hypothesis and ugly facts. – Oxford Univ. Press.

Christian, J. J. 1950. The andro-pituitary system and population cycles in small mammals. – J. Mammal. 31: 247–259.

Christian, J. J. 1980. Endocrine factors in population regulation. – In: Cohen, M. N., Malpass, R. S., and Klein, H. G. (eds.), Biosocial mechanism in population regulation. Yale Univ. Press, pp. 55–115.

Elton, C. S. 1924. Periodic fluctuations in numbers of animals: their causes and effects. – J. Exp. Biol. 2: 119–163.

Elton, C. S. 1942. Voles, mice and lemmings: problems in population dynamics. – Clarendon Press.

Gilbert, B. S. and Krebs, C. J. 1981. Effects of extra food on *Peromyscus* and *Clethrionomys* populations in the southern Yukon. – Oecologia 51: 326–331.

Gilbert, C. et al. 2010. One for all and all for one: the energetic benefits of huddling in endotherms. – Biol. Rev. 85: 545–569.

Gilg, O. et al. 2003. Cyclic dynamics in a simple vertebrate predator-prey community. – Science 302: 866–868.

Ginzburg, L. R. and Taneyhill, D. E. 1994. Population cycles of forest Lepidoptera - a maternal effect hypothesis. – J. Anim. Ecol. 63: 79–92.

Gliwicz, J. 1997. Space use in the root vole: Basic patterns and variability. – Ecography 20: 383–389.

Glorvigen, P. et al. 2012a. Settlement in empty versus occupied habitats: an experimental study on bank voles. – Popul. Ecol. 54: 55-63.

Glorvigen, P. et al. 2012b. The role of colonization in patchy population dynamics of a cyclic vole species. – Manuscript.

Glorvigen, P. et al. 2012c. Relative importance of habitat geometry, habitat quality, population size and environmental stochasticity on occupancy dynamics in a riparian mainland-island root vole metapopulation. – Manuscript.

Gundersen, G. et al. 2001. Source-sink dynamics: how sinks affect demography of sources. – Ecol. Lett. 4: 14–21.

Haapakoski, M. and Ylonen, H. 2010. Effects of fragmented breeding habitat and resource distribution on behavior and survival of the bank vole (*Myodes glareolus*). – Popul. Ecol. 52: 427–435.

Halle, S. 1988. Avian predation upon a mixed community of common voles (*Microtus-arvalis*) and wood mice (*Apodemus-sylvaticus*). – Oecologia 75: 451–455.

Hansen, T. F. et al. 1999. Interspecific and intraspecific competition as causes of direct and delayed density dependence in a fluctuating vole population. – PNAS 96: 986–991.

Hanski, I. et al. 2001. Small-rodent dynamics and predation. – Ecology 82: 1505–1520.

Hansson, L. 1984. Predation as the factor causing extended low-densities in microtine cycles. – Oikos 43: 255–256.

Hansson, L. 1998. Mast seeding and population dynamics of rodents: one factor is not enough. – Oikos 82: 591–594.

Hansson, L. and Henttonen, H. 1985. Gradients in density variations of small rodents - the importance of latitude and snow cover. – Oecologia 67: 394–402.

Hayes, L. D. 2000. To nest communally or not to nest communally: a review of rodent communal nesting and nursing. – Anim. Behav. 59: 677–688.

Henttonen, H. 1987. The impact of spacing behavior in microtine rodents on the dynamics of least weasels *Mustela-nivalis* - a hypothesis. – Oikos 50: 366–370.

Heske, E. J. and Bondrup-Nielsen, S. 1990. Why spacing behavior does not stabilize density in cyclic populations of microtine rodents. – Oecologia 83: 91–98.

Heske, E. J. and Jensen, P. M. 1993. Social structure in *Lemmus lemmus* during the breeding season. – In: Stenseth, N. C. and Ims, R. A. (eds.), The biology of lemmings. Academic Press, pp. 387–395.

Hestbeck, J. B. 1982. Population regulation of cyclic mammals: the social fence hypothesis. – Oikos 39: 157–163.

Huitu, O. et al. 2003. Winter food supply limits growth of northern vole populations in the absence of predation. – Ecology 84: 2108–2118.

Ims, R. A. 1987a. Responses in spatial-organization and behavior to manipulations of the food resource in the vole *Clethrionomys-rufacanus*. – J. Anim. Ecol. 56: 585–596.

Ims, R. A. 1987b. Male spacing systems in Microtine rodents. – Am. Nat. 130: 475–484.

Ims, R. A. 1988. Spatial clumping of sexually receptive females induces space sharing among male voles. – Nature 335: 541–543.

Ims, R. A. and Andreassen, H. P. 2000. Spatial synchronization of vole population dynamics by predatory birds. – Nature 408: 194–196.

Ims, R. A. and Andreassen, H. P. 2005. Density-dependent dispersal and spatial population dynamics. – Proc. R. Soc. B 272: 913–918.

Ims, R. A. et al. 2011. Determinants of lemming outbreaks. – PNAS 108: 1970–1974.

Inchausti, P. and Ginzburg, L. R. 1998. Small mammals cycles in northern Europe: patterns and evidence for a maternal effect hypothesis. – J. Anim. Ecol. 67: 180–194.

Kausrud, K. L. et al. 2008. Linking climate change to lemming cycles. – Nature 456: 93–98.

Kendall, B. E. et al. 1998. The macroecology of population dynamics: taxonomic and biogeographic patterns in population cycles. – Ecol. Lett. 1: 160–164.

Korpela, K. et al. 2011. Does personality in small rodents vary depending on population density? – Oecologia 165: 67–77.

Korpimaki, E. 1985. Prey choice strategies of the kestrel *Falco-tinnunculus* in relation to available small mammals and other Finnish birds of prey. – Ann. Zool. Fenn. 22: 91–104.

Korpimaki, E. and Norrdahl, K. 1998. Experimental reduction of predators reverses the crash phase of small-rodent cycles. – Ecology 79: 2448–2455.

Korpimaki, E. et al. 2004. The puzzles of population cycles and outbreaks of small mammals solved? – Bioscience 54: 1071–1079.

Korslund, L. and Steen, H. 2006. Small rodent winter survival: snow conditions limit access to food resources. – J. Anim. Ecol. 75: 156–166.

Krebs, C. J. 1978. A review of the Chitty hypothesis of population regulation. – Can. J. Zool. 56: 2463–2480.

Krebs, C. J. 1979. Dispersal, spacing behavior, and genetics in relation to population fluctuations in the vole *Microtus-townsendii*. – Fortschritte Der Zoologie 25: 61–77.

Krebs, C. J. 1996. Population cycles revisited. – J. Mammal. 77: 8–24.

Krebs, C. J. 2011. Of lemmings and snowshoe hares: the ecology of northern Canada. – Proc. R. Soc. B 278: 481–489.

Krebs, C. J. and Myers, J. H. 1974. Population cycles in small mammals. – Adv. Ecol. Res. 8: 267–399.

Krebs, C. J. et al. 1995. Can changes in social-behavior help to explain house mouse plagues in Australia. – Oikos 73: 429–434.

Krebs, C. J. et al. 2010. Do changes in berry crops drive population fluctuations in small rodents in the southwestern Yukon? – J. Mammal. 91(2): 500-509.

Laine, K. and Henttonen, H. 1983. The role of plant-production in microtine cycles in northern Fennoscandia. – Oikos 40: 407–418.

Lambin, X. and Krebs, C. J. 1991. Can changes in female relatedness influence microtine population-dynamics. – Oikos 61: 126–132.

Lambin, X. and Krebs, C. J. 1993. Influence of female relatedness on the demography of Townsends vole populations in spring. – J. Anim. Ecol. 62: 536–550.

Lambin, X. and Yoccoz, N. G. 1998. The impact of population kin-structure on nestling survival in Townsend's voles, *Microtus townsendii*. – J. Anim. Ecol. 67: 1–16.

Lambin, X. et al. 1992. Spacing system of the tundra vole (*Microtus-oeconomus*) during the breeding-season in Canada western Arctic. – Can. J. Zool. 70: 2068–2072.

Lambin, X. et al. 2001. Dispersal, intraspecific competition, kin competition and kin facilitation: a review of the empirical evidence. – In: Clobert, J., Danchin, E., Dhondt, A. A., and Nichols, J. D. (eds.), Dispersal. Oxford Univ. Press, pp. 110–122.

Lambin, X. et al. 1998. Spatial asynchrony and periodic travelling waves in cyclic populations of field voles. – Proc. R. Soc. B 265: 1491–1496.

Le Galliard, J.-F. et al. 2012. Patterns and processes of dispersal behaviour in arvicoline rodents. – Molecular Ecology 21: 505–523.

Lidicker, W. Z. 1973. Regulation of numbers in an island population of the California vole, a problem in community dynamics. – Ecol. Monogr. 43: 271–302.

Lidicker, W. Z. 1988. Solving the enigma of microtine cycles. – J. Mammal. 69: 225–235.

Lin, Y. T. K. and Batzli, G. O. 2001. The influence of habitat quality on dispersal demography, and population dynamics of voles. – Ecol. Monogr. 71: 245–275.

Lindstrøm, J. et al. 2001. From arctic lemmings to adaptive dynamics: Charles Elton's legacy in population ecology. – Biol. Rev. 76: 129–158.

Loe, L. E. et al. 2009. Negative density-dependent emigration of males in an increasing red deer population. – Proc. R. Soc. B 276: 2581–2587.

Lucia, K. E. et al. 2008. Philopatry in prairie voles: an evaluation of the habitat saturation hypothesis. – Behav. Ecol. 19: 774–783.

Mappes, T. et al. 1993. Selective avian predation on a population of the feld vole, *Microtus-agrestis* - greater vulnerability of males and subordinates. – Ethol. Ecol. Evol. 5: 519–527.

Matthiopoulos, J. et al. 1998. Models of red grouse cycles. A family affair? – Oikos 82: 574–590.

Matthiopoulos, J. et al. 2000. The kin-facilitation hypothesis for red grouse population cycles: Territory sharing between relatives. - Ecol. Model. 127: 53-63.

Matthiopoulos J. et al. 2002. The kin facilitation hypothesis for red grouse population cycles: territorial dynamics of the family cluster. - Ecol. Model. 147: 291-307.

Matthiopoulos, J. et al. 2003. Territorial behaviour and population dynamics in red grouse Lagopus agopus scoticus. II. Population models. - J. Anim. Ecol. 72: 1083-1096.Mougeot, F. et al. 2003. The effect of aggressiveness on the population dynamics of a territorial bird. – Nature 421: 737–739.

New, L. F. et al. 2009. Fitting models of multiple hypotheses to partial population data: investigating the causes of cycles in red grouse. – Am. Nat. 174: 399–412.

Nie, H. and Liu, J. 2005. Regulation of root vole population dynamics by food supply and predation: a two-factor experiment. – Oikos 109: 387–395.

Oksanen, T. et al. 2008. Arctic lemmings, *Lemmus* spp. and *Dicrostonyx* spp.: integrating ecological and evolutionary perspectives. – Evol. Ecol. Res. 10: 415–434.

Opperbeck, A. et al. 2012. Infanticide and Population Growth in the Bank Vole (*Myodes glareolus*): The Effect of Male Turnover and Density. – Ethology 118: 178–186.

Ostfeld, R. S. 1985. Limiting resources and territoriality in microtine rodents. – Am. Nat. 126: 1–15.

Reid, D. G. et al. 1995. Limitation of collared lemming population-growth at low-densities by predation mortality. – Oikos 73: 387–398.

Reid, D. G. et al. 2012. Lemming winter habitat choice: a snow-fencing experiment. – Oecologia 168: 935–946.

Rémy, A. 2011. Linking behaviour with individual traits and environmental conditions, and the consequences for small rodent populations. University of Oslo, Oslo.

Smith, M. J. et al. 2008. The effects of density-dependent dispersal on the spatiotemporal dynamics of cyclic populations. – J. Theor. Biol. 254: 264–274.

Steen, H. et al. 1990. Predators and small rodent cycles - an analysis of a 79-year time-series of small rodent population fluctuations. – Oikos 59: 115–120.

Stenseth, N. C. 1978. Is female biased sex-ratio in wood lemming *Myopus-schisticolor* maintained by cyclic inbreeding? – Oikos 30: 83–89.

Stenseth, N. C. and 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.

Stenseth, N. C. and Ims, R. A. (eds.), 1993. The biology of lemmings. Academic Press.

Stenseth, N. C. et al. 1996. Is spacing behaviour coupled with predation causing the microtine density cycle? A synthesis of current process-oriented and pattern-oriented studies. – Proc. R. Soc. B 263: 1423–1435.

Stockley, P. and Bro-Jørgensen, J. 2011. Female competition and its evolutionary consequences in mammals. – Biol. Rev. 86: 341–366.

Støen, O. G. et al. 2006. Inversely density-dependent natal dispersal in brown bears *Ursus arctos*. – Oecologia 148: 356–364.

Sundell, J. 2006. Experimental tests of the role of predation in the population dynamics of voles and lemmings. – Mammal Rev. 36: 107–141.

Sundell, J. et a. 2012. Spatio-temporal patterns of habitat use in voles and shrews modified by density, season and predators. - J. Anim. Ecol. 81: 747-755.

Sutherland, D. R. et al. 2005. Kin interactions and changing social structure during a population outbreak of feral house mice. – Mol. Ecol. 14: 2803–2814.

Tast, J. 1966. The root vole, *Microtus oeconomus* (Pallas), as an inhabitant of seasonally flooded land. – Ann. Zool. Fenn. 3: 127–170.

Tkadlec, E. and Zejda, J. 1998a. Density-dependent life histories in female bank voles from fluctuating populations. – J. Anim. Ecol. 67: 863–873.

Tkadlec, E. and Zejda, J. 1998b. Small rodent population fluctuations: The effects of age structure and seasonality. – Evol. Ecol. 12: 191–210.

Turchin, P. 2003. Voles and other rodents. – In: Turchin, P. (ed.), Complex population dynamics. Princeton Univ. Press, pp. 296–343.

Turchin, P. and Batzli, G. O. 2001. Availability of food and the population dynamics of arvicoline rodents. – Ecology 82: 1521–1534.

Turchin, P. and Hanski, I. 2001. Contrasting alternative hypotheses about rodent cycles by translating them into parameterized models. – Ecol. Lett. 4: 267–276.

Turchin, P. et al. 2000. Are lemmings prey or predators? – Nature 405: 562–565.

Warkowska-Dratna, H. and Stenseth, N. C. 1985. Dispersal and the microtine cycle: comparison of two hypotheses. – Oecologia 65: 468–477.

Wiklund, C. G. 1996. Determinants of dispersal in breeding merlins (*Falco columbarius*). – Ecology 77: 1920–1927.

Wolff, J. O. 1993. Why are female small mammals territorial? – Oikos 68: 364–370.

Wolff, J. O. 1997. Population regulation in mammals: An evolutionary perspective. – J. Anim. Ecol. 66: 1–13.

Wolff, J. O. and Peterson, J. A. 1998. An offspring-defense hypothesis for territoriality in female mammals. – Ethol. Ecol. Evol. 10: 227–239.

Ylonen, H. and Viitala, J. 1991. Social overwintering and food distribution in the bank vole *Clethrionomys-glareolus*. – Holarctic Ecol. 14: 131–137.

Ylonen, H. et al. 1990. Different demography of friends and strangers - an experiment on the impact of kinship and familiarity of *Clethrionomys-glareolus*. – Oecologia 83: 333–337.

Ylonen, H. et al. 1997. Infanticide in the bank vole (*Clethrionomys glareolus*): Occurrence and the effect of familiarity on female infanticide. – Ann. Zool. Fenn. 34: 259–266.

Figure legends

Figure 1. The model showing the increase phase as an interaction between resource

patchiness and social factors, and the crash phase as an interaction between predation and

social factors.

Figure 1

Increasing vole populations
- *Stable social groups (possibly matriarchies)*
- *High dispersal rate leading to successful colonization of vacant patches*
- *High survival and reproduction*
- *Even sex ratio and a high proportion of young*

Predation, initially of adult dominant males

Infanticide

Mortality of adult social females

Increased movements

High recruitment

Socialisation

Resource patchiness

Increase phase

Crash phase

Decreasing vole populations
- *Social disruption*
- *High dispersal rate associated with high mortality*
- *Low recruitment and survival*
- *Adult segment female biased sex ratio*
- *A high proportion of adults (females)*