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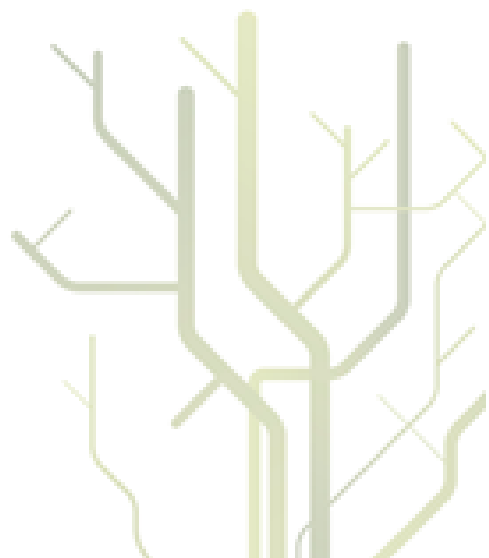
Vole population cycles and the role of colonisation

Petter Glorvigen

A dissertation for the degree of
Philosophiae Doctor

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List of papers

This thesis is based on the following original article and manuscripts which are indicated in the text by their roman numerals I – IV below.

I   Glorvigen, P., Bjørnstad O.N., Andreassen, H.P. and Ims, R.A. 2012. Settlement in empty versus occupied habitats: an experimental study on bank voles. *Population Ecology* 54:55-63.

II   Glorvigen, P., Gundersen, G., Andreassen, H.P. and Ims, R.A. The role of colonization in patchy population dynamics of a cyclic vole species. *Submitted to Oecologia*.

III   Glorvigen, P., Andreassen, H.P. and Ims, R.A. Relative importance of habitat geometry, habitat quality, population size and environmental stochasticity on occupancy dynamics in a riparian mainland-island root vole metapopulation. *Submitted to PLOS ONE.*

IV   Andreassen, H.P., Glorvigen, P., Rémy, A. and Ims, R. A. New views on how population-intrinsic and community-extrinsic processes interact during the vole population cycles. *Submitted to Oikos.*

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Abstract

The multiannual population cycles of small rodents have triggered one the most intense debates within the field of population ecology. Opposing views from proponents of either population-intrinsic or community-extrinsic factors as the cycle generating mechanisms have influenced the debate for more than 80 years. However, for decades population ecologists have argued that solving the puzzle depend on multifactorial approaches, combining intrinsic and community-level processes. For simplicity, population cycles are often described as a four-phase process; the peak phase, the crash phase, the low phase and the increase phase. A well-known challenge when studying small rodent dynamics is the apparent absence of individuals during the low phase and some of the dispute on the cause of population cycles may originate from the fact that most studies addressing vole and lemming behaviour and demography are only conducted at high to moderate population densities.

Overall this thesis aims to (1) present new insight of relevance to the least studied phase(s) of the vole population cycles: specifically, the role of colonisation processes in the transition from small isolated populations in the low-phase to the spatially extensive populations in the peak phase of the cycle and (2) to provide an updated view (based on results from this thesis and some other recent experiments focusing on sociality) on how population-intrinsic and community-extrinsic processes may interact during the vole population cycles.

The first experiment demonstrated that colonisation is a beneficial strategy in female bank voles (*Myodes glareolus*) compared to immigration. The second experiment demonstrated that the first born cohort of root voles (*Microtus oeconomus*) emigrating in early summer have a high capacity for colonising spatially scattered habitats – a capacity that explains the fast recolonisation of empty habitat space following crashes in cyclic populations. These experimental results also gave evidence of the presence of social fences around high quality habitats at low population density, and thus in the increase phase, voles seem to actively search out vacant habitats and settle in them conditional on habitat quality and population density. An observational study of a riparian mainland-island root vole metapopulation confirmed that such patchy populations with cyclic dynamics may be subject to extensive occupancy dynamics. However, owing to high capacities for dispersal and habitat tracking, voles rapidly colonised the high quality islands across the entire metapopulation landscape that previously had gone extinct due to demographic (small population size) and environmental (high water levels) stochasticity. Together, the experimental and observational studies show that spatially

scattered (sub)populations that have survived the crash phase are able (under otherwise benign conditions) to provide colonists, even to remote habitat patches imbedded in a hostile matrix, and thus pave the way to a new increase and peak phase. It is noteworthy however that metapopulation persistence may be at risk if the source populations no longer regularly facilitate a high number of young colonisers due to climate change (degraded snow cover properties) or worsened matrix conditions (fragmentation).

The updated view on the causes of population cycles in voles emphasises the important role of dispersal (colonisation) and sociality in all phases of the cycle. It is claimed that both dispersal and sociality may confer opposing demographic effects in the increase and crash phase of the cycle. It is not claimed that intrinsic mechanisms, either alone or in interactions with extrinsic factors, are necessary for generating multiannual cycles. Given the present empirical and theoretical evidence, there is ample evidence that extrinsic factors are the key drivers of population density cycles. The argument is rather that intrinsic factors may contribute to shaping rodent populations dynamics and by taking this into consideration one may be better able to explain why the prevalence of population cycles and associated phenomena vary in time and space. It is also suggested that different innate propensities for sociality and dispersal among different rodent species may be related to inter-specific variation in topology of the cycles (i.e. cycle shape and amplitude) and degree of spatial population synchrony.

Contents

1. Introduction and background

1.1. The challenge of explaining small rodent population cycles

Ever since Elton (1924, 1942) - one of the pioneers of modern ecology – first wrote about the periodic changes in abundance of small mammals, unravelling the causes behind this phenomenon has been the prime target of many ecologists (Lindstrøm et al. 2001). One of the main reasons for this long-standing interest is that population cycles (i.e. regular high amplitude oscillations of density) represent a regular flow of resources and disturbances fundamental to terrestrial ecosystem functioning (e.g. Ims and Fuglei 2005). Investigating population cycles also provides basic ecological knowledge about the mechanisms of population regulation and community dynamics. However, it is only for a few carefully studied species/populations that ecologists have managed to approach something like a consensus on the causes of cyclicity (Krebs et al. 2001, Gilg et al. 2003). Even in the case of comprehensive experimental and observational studies conducted on snowshoe hare dynamics in Canada over more than 80 years, synthesising the results into firm conclusions has not been an easy task (Keith 1990, Krebs et al. 1995, Krebs 2011). In his latest review, Krebs (2011) points to many critical gaps in the current knowledge about snowshoe hares. The challenge is even bigger when attempting to approach general conclusions on the causes behind small rodent cycles (Stenseth and Ims 1993b, Krebs 1996, Krebs 2011). This is because the list of hypotheses being forwarded is more extensive than in any other taxon and because of the often conflicting empirical evidence (e.g. Stenseth and Ims 1993a). There are many different species of small rodents which may or may not be cyclic, and even for the same species the occurrence of cycles show huge spatiotemporal variation (e.g. Henden et al. 2009). This complexity may explain why the causes of population cycles are still debated despite the fact that species like voles and lemmings are by far the most studied taxa with cyclic dynamics (e.g. Krebs 1996, Graham and Lambin 2002, Oli 2003a, b, Korpimaki et al. 2005, Inchausti and Ginzburg 2009, see also Stenseth 1999 for an overveiw of the early debate).

Population cycles are, for simplicity, often described as a four-phase process; the peak phase, the crash phase, the low phase and the increase phase. A well-known challenge when studying small rodent dynamics is the apparent absence of individuals during the low phase. Capturing individuals during the low phases is demanding even for experienced field ecologists. This contrasts with the peak phases in which even laypeople observe numerous individuals over large areas. Hence, field studies

targeting cyclic lemming and vole dynamics in boreal and arctic regions often result in time series consisting of zero (or close to zero) observations in some years and very high capture rates in other years (e.g. Kausrud et al. 2008). One consequence of this apparent absence of individuals is that many population models rest on the assumption that local populations survive only in a few high quality patches during population lows and that individuals from these source patches propagate the increase phase (Stenseth 1978, Charnov and Finerty 1980, Warkowska-Dratna and Stenseth 1985; see also Stenseth and Lomnicki 1990, Andreassen et al. 2002). In the low phase, irrespective of the spatial distribution of the few remaining local populations, lots of empty habitats exist. In the peak phase, new populations are founded in these previously empty habitats (Löfgren 1995, Henden et al. 2011). A vole population cycle could thus be described as a sort of metapopulation dynamics governed by frequent colonisation and extinction events in local habitat patches. Dispersal from source populations and colonisation of empty population space characterises the increase phase, while extinction of populations in local habitat patches characterises the crash phase.

To a certain extent the remaining uncertainty about the causes of small rodent cycles may originate from the fact that most studies addressing vole and lemming behaviour (i.e. dispersal, habitat selection, sociality, infanticide) and demography are conducted at high to moderate population densities. Indeed, investigations of the processes involved in the succession of events (both on the individual level as well as at the level of populations and metapopulations) from the crash with small, scattered local populations to the peak phase with a saturated landscape, is rarely targeted in any studies. The lack of knowledge about voles and lemmings living at low population densities has previously been termed as *the Achilles heel for most of the proposed models of cycles* (Boonstra et al. 1998). Providing knowledge about the mechanisms governing colonisation (and spatial spread), as well as the role of colonisation in patchy population dynamics is therefore important for the general understanding of the causes of population cycles. Indeed, it has been predicted that a pronounced drive and ability for effective colonisation should have evolved as an important life history trait in patchily distributed voles with cyclic dynamics (Ebenhard 1990).

1.2. Investigating the increase phase

If local populations of small rodents are kept in isolation for an extended period of time they resemble the situation of many endangered species. Species experiencing low densities are typically divided

into isolated populations which are particularly vulnerable to variation in individual vital rates (demographic stochasticity), environmental stochasticity and random catastrophic events (Lande 1993). In addition come the longer term genetic consequences of isolation, like inbreeding depression and loss of genetic diversity (Frankham 2005). Despite this vulnerability, local populations may persist because immigration (settlement in an established population) counteracts the negative effects of small population size (Brown and Kodric-Brown 1977), and colonisation (settlement in empty habitats) buffers local extinctions (Hanski and Gilpin 1991). Hence, colonisation and immigration are vital factors affecting the viability of species with a patchy distribution (*sensu* Hanski 1999).

Colonisation and immigration characterise the final phase of a successful dispersal process (e.g. Ims and Yoccoz 1997). While the scientific literature on dispersal has focused much on determinants of emigration there has been less focus on determinants of settlement (e.g. Clobert et al. 2001, Bowler and Benton 2005). This may have to do with the practical difficulties in identifying potential dispersers in their natal habitat and following them throughout the dispersal process (Ims and Yoccoz 1997). The process of settlement of dispersers has however been focused on by scientists working with habitat selection (Hildén 1965, Stamps 1994). Following Stamps (2001), habitat selection might be divided into three stages; search, settlement and residency in the new habitat. The highest costs are related to search and settlement, while the benefits are paid in the resident period (Stamps 2001, Bonte et al. 2012). Habitat selection theory originates from the ideal free distribution (IDF) model of Fretwell and Lucas (1970) which assumes that conspecifics compete for resources and that the individual fitness declines as a function of density. On the other hand, the original theory of Allee (1951) predicts a positive relationship between density and fitness at low to moderate densities because of socially induced fitness gains related to residency among conspecific (Stephens et al. 1999, Courchamp et al. 2008). Examples of such benefits are a reduced risk of predation, increased access to mates, more efficient social thermoregulation or protection against infanticidal conspecifics (e.g. Rosenzweig 1981, Agrell et al. 1998, Kuussaari et al. 1998, Morris 2002, Stephens et al. 2002, Molnar et al. 2008, Brashares et al. 2010). Conspecifics may also function as indicators of habitat quality. If individuals have the ability to prospect conspecific breeding success, this may function as a cue for settlement (Danchin et al. 1998). In addition, using conspecifics as cues of habitat quality may reduce search costs (Stamps 2001). Despite the fact that social factors may determine settlement, social components might also hinder settlement due to territorial behaviour and social fences (Hestbeck 1982).

Conspecific attraction has been documented in many taxonomic groups, especially colonial and territorial birds (Danchin et al. 1998, Ward and Schlossberg 2004), but data on settlement processes in territorial mammals is almost totally lacking and the empirical information that does exist suggests social fence effects rather than conspecific attraction (Gundersen et al. 1999, McGuire et al. 2009). In **paper I** we translocated bank voles (*Myodes glareolus*) onto an island in a two-stage low density experiment to test whether presence of conspecifics or habitat quality determines settlement and reproduction in colonising and immigrant females.

At least three assumptions are commonly made when predicting recovery from cyclic population lows in small rodents. 1) The few remaining source patches (local populations) must have escaped from the factors enforcing low density (e.g. a predator pit; Boonstra et al. 1998), so that 2) they harbour individuals prone to disperse when the environmental conditions allow for emigration, so that 3) suitable empty patches within dispersal range are colonised with individuals that are capable of establishing a new (sub)population with positive population growth. In **paper II** we report from an experiment with root voles (*Microtus oeconomus*), specifically targeted at quantifying the process of colonisation of empty patches from distant source patches and its resultant effect on local vole deme size variation in a patchy landscape. Three experimental factors, habitat quality (1), predation risk (2) and inter-patch distance (3) were employed to test their effect on post-colonisation deme sizes and on final deme performance at the end of the reproductive season.

In the wild, small rodents live in heterogeneous landscapes. As described above, it is often assumed that voles are present in only a few high quality patches in the early increase phase, while they are present in nearly all habitats in the peak phase (e.g. Bondrup-Nielsen and Ims 1988b, Lidicker 1988). Habitat patches may also vary in suitability within seasons or due to environmental stochasticity, resulting in frequent colonisation and extinction events in small rodent metapopulations that may not be related to the cycle generating mechanism(s). It is difficult to identify clearly distinct habitat patches (i.e. a metapopulation) in, for example, a forest mosaic, while it is much easier (for terrestrial species) for island systems (archipelagos) in water bodies (oceans, lakes and rivers). For this reason such island systems have served an important role in the study of colonisation (and extinction) processes since MacArthur and Wilson launched their theory of island biogeography (MacArthur and Wilson 1967). In **paper III** we identified a metapopulation constituting 15 islands and the mainland in a river system. This island-mainland riparian system was also expected to be subject

to frequent extinction events due to occasional high water levels (flooding) during snow melt and heavy rainfall. By monitoring the occupancy dynamics on these islands and the population size on the mainland we were able to identify important mechanisms influencing colonisation and extinction, thus resembling the essential spatial dynamics of cyclic vole populations. We aimed to investigate the influence of island geometry, habitat quality, population size and environmental stochasticity (i.e. water level) on colonisation and extinction. By applying a recent statistical modelling approach we were also able to quantify and adjust for the possibility of false absence (i.e. that individuals are present even though they are not detected, *sensu* the challenge of apparent absence (zeros) in most time series of vole and lemming abundance).

1.3. Mechanisms involved in population cycles

Although small rodent population dynamics may pessimistically be considered too complex for single explanations, some well-documented and common patterns of evidence have emerged over the years. The causes of cyclic population fluctuations can roughly be divided in two categories, with historically strong proponents on both sides. Originating from the hypotheses of Chitty (1952, 1960, 1967) and Charnov and Finery (1980, see also Charnov 1981) proponents of *intrinsic* processes have investigated, for example, social organisation and spacing behaviour as potential mechanisms involved in the populations cycles (e.g. Krebs 1979, Boonstra and Hogg 1988, Lambin and Krebs 1991, Lidicker and Ostfeld 1991, Ostfeld et al. 1993, Boonstra 1994, Löfgren 1995, Boonstra et al. 1998, Wolff and Peterson 1998, Sinclair et al. 2003). On the other side, proponents of *extrinsic* processes have focused much on predation and food (Batzli 1986, Hansson and Henttonen 1988, Selås 1997, Hanski et al. 2001, Gilg et al. 2003). Perhaps the most common and best documented view is that predation is the only singular factor sufficient to cause vole population cycles (e.g. Hansson and Henttonen 1985, Hanski et al. 2001, Gilg et al. 2003, Turchin 2003, Begon et al. 2006, but see Krebs 1996 and Ergon et al. 2011). Long-term monitoring records of voles, lemmings and their closely related predators have shown that the populations normally peak every 3-5 years, with a spatial gradient of noncyclic populations in the far south, through relatively short intervals between peaks in the central parts ($3 - 4$ years) and with the longest intervals in the far north ($4 - 5$ years; Bjørnstad et al. 1995). The functional response of generalist predators causes predation rates that fluctuate with vole numbers, while the delayed numerical response in specialist predators also causes

high predation rates when vole abundance is declining. The spatial gradient in cyclicity is thus attributed to the predator community assemblage with abundant generalist predators in the south and more specialist predators in the north (Hanski et al. 1991).

However, voles are obviously affected by the quality and quantity of their food resources. Supplementation experiments show positive effects of food on demographic traits (e.g. early onset of reproduction, see reveiw in Boutin 1990). Correlative studies show that small rodent populations may fluctuate with the quantity and quality of their food sources (e.g. Laine and Henttonen 1983, Batzli 1985, Seldal et al. 1994, Ostfeld et al. 1996, Selås 1997, Boonstra and Krebs 2006, Selås 2006, Boonstra and Krebs 2012). Explanations for such correlations in cyclic species are often pulsed food supplies (e.g. masting events in vital food plants) facilitating the increase phase, while deteriorating food resources (quality or quantity) may initiate the decrease phase (e.g. Krebs et al. 2010, Boonstra and Krebs 2012). Deteriorating food resources have also been used to explain maternal effects causing low reproductive output for an extended period of time, thus prolonging the low phase. Maternal effects are normally termed as a delayed density dependent intrinsic factor as there is something "wrong" with individuals (e.g. late onset of reproduction) even though the food resources are ample in the low phase (e.g. Ergon et al. 2011).

Population cycles are often spatially synchronous within regions and have similar cycle period length (Bjørnstad et al. 1999, Henden et al. 2009). Evidence suggests that this synchrony is likely caused by large-scale climatic conditions or nomadic avian specialist predators tracking local variation in vole abundance (Ranta et al. 1995, Ims and Andreassen 2000, Huitu et al. 2005). There is little evidence that dispersal or other behavioural characteristics may act as synchronising agents. This is partly because synchronised dynamics have been recorded on a much larger scale than what is considered as the maximum dispersal range in any vole species (e.g. Ims and Andreassen 2000, but see Steen et al. 1996 about the synchronising effect of dispersal on smaller scales) and partly because it has proven difficult to identify mechanism synchronising the behaviour in ways that alter demographic rates (e.g. Stenseth and Lomnicki 1990).

Although the debate about the mechanisms involved in population cycles has been heavily influenced by proponents of either intrinsic or community-extrinsic processes, single factor approaches have commonly been claimed as too simplistic. For more than 30 years, ecologist have argued that the causes of population cycles are best explained by combining intrinsic and extrinsic factors

(Bondrup-Nielsen and Ims 1988b, a, Lidicker 1988, Krebs 1996, Stenseth et al. 1996, Boonstra et al. 1998, Hansson 1998, Stenseth 1999, Aars and Ims 2002).

At our research station at Evenstad, small rodent experiments have been conducted for more than 20 years. Over the years extensive knowledge has been acquired about root vole demography (Johannesen and Ims 1996, Ims and Andreassen 1999, Aars and Ims 2000), space use (Hansteen et al. 1997, Andreassen et al. 1998, Hovland et al. 1999), dispersal behaviour (Bjørnstad et al. 1998, Gundersen and Andreassen 1998, Johannesen and Andreassen 1998) and life history strategies (Aars et al. 1995, Ims 1997, Johannesen and Andreassen 1998). Although the focus has been on how habitat fragmentation directly affects population performance, it has become clear that habitat manipulations work through some mechanism of spacing behaviour and/or social organisation, indirectly causing the measurable effect on demography and population performance. Recently experiments on another species, the bank vole, have been conducted to explore in more detail how spatial distribution of food resources affect social organisation, demography and population performance (Rémy 2011). Interestingly, patchily distributed high quality food within experimental plots not only caused aggregation of females, as shown in other studies (e.g. Ims 1987), but local populations of social females also reached higher numbers than populations receiving evenly distributed food (Rémy 2011). Because voles (and lemmings) aggregate in survival pockets under the snow in winter (Korslund and Steen 2006, Reid et al. 2012), improved food conditions (e.g. favourable snow conditions with little ice and/or ample food resources) may facilitate socialisation, early recruitment and the rapid population increase in early spring necessary for attaining peak phase densities. As in these studies on the effect of sociality and spatial organisation on population performance, new insight of relevance for understanding the role of individual behaviour (i.e. intrinsic mechanisms) in the generation of population cycles was achieved in the studies of colonisation (paper I-III) constituting the main empirical part of the present thesis. Together, these pieces of knowledge have enlightened our view on the puzzle of vole and lemming cycles. In **paper IV** we have synthesised the best of our knowledge from the experiments conducted at Evenstad Research Station, together with the large set of other experimental and observational studies on voles and lemmings, in a new updated view on how population-intrinsic and community-extrinsic processes may interact during the vole population cycles.

1.4. Aims of the thesis

This thesis aims to (1) present new insight of relevance to the least studied phase(s) of the vole population cycles: specifically the role of colonisation processes in the transition from small isolated populations in the low-phase to the spatially extensive populations in the peak phase of the cycle (paper I-III) and (2) in the light of our recent experimental results, to provide an updated view of how population-intrinsic and community-extrinsic processes may interact during the vole population cycles (paper IV).

2. Study species

Both study species (root voles and bank voles) are common on the Fennoscandian peninsula and known to exhibit multiannual population cycles in the north. Root voles are considered to be habitat specialists that prefer moist and meadow-like habitats along river banks, creeks, around small forest lakes and abandoned agricultural fields (Tast 1966, Lambin et al. 1992, Henden et al. 2011). They are considered to be graminivorous (Tast 1966) although a new study suggests that they also consume a lot of forbs (Soininen et al. 2009). Bank voles are less restricted to specific habitats, especially in high density years (Löfgren 1995). They are abundant in mature forest, but are also found on clear-cuts and on meadows in our study areas (Gorini et al. 2011). Bank voles are omnivorous. Their diet is dominated by seeds, forbs, berries, fungi and grass (Hansson 1985). Both species rarely live for more than a year. The reproductive potential is high, with up to four litters during the reproductive season (April to October). Each litter commonly consists of 4-7 offspring (Ims 1997, Oksanen et al. 2001). Natal dispersal dominates and breeding dispersal is rare in both species (Löfgren 1995, Andreassen and Ims 2001). Their dispersal capacity is assumed to be high (Steen et al. 2005), although the true dispersal range is not known in either species. Because of their dramatic spatiotemporal population dynamics and adaptation to patchy habitats, both species are well suited to experimental studies of patchy population dynamics (Ims et al. 1993, Wiens et al. 1993).

Adult bank vole captured in the preferred mature forest habitat dominated by grass, forbs and berry carrying dwarf shrubs in the ground layer (Photo: Petter Glorvigen)

Adult root vole captured in the preferred habitat consisting of dense grass vegetation on moist nutritional soil close to the water (Photo: Petter Glorvigen)

3. Methods

In this thesis I use a combination of three of the main study approaches used in ecological research: 1) field experiments to test specific hypothesis on the study targets' responses to specific ecological factors applied as experimental treatments (Paper I and II) and 2) an observational study of a natural system where predicted covariates to the observed response variables were sampled and modelled to determine whether estimated parameters were consistent with theory (Paper III) and 3) a literature review synthesising the current state of knowledge, concluding with a list of testable predictions for future research (Paper IV).

3.1. Paper I

This field experiment was conducted on an island in a lake in south-east Norway. After removal of the native population, translocated bank voles from the mainland were introduced at two stages in replicated trials, mimicking colonising and immigrant females, respectively. In the first stage, settlement of colonisers was investigated in relation to simulated deserted home ranges of reproductive females (SDHR; petri-dishes with urine soaked sawdust from lactating females). In the second stage, immigrant settlement was investigated in relation to resident conspecific females (i.e. the females that had continued their residency from the colonisation stage). Animals were monitored by live trapping to determine individual home range size and location of home range centres (minimum convex polygon). Each stage lasted for 12 days and each replicate was terminated by removal of all females. The experiment had 8 replicates over 3 years. All females removed from the island after the immigration stage (residents and immigrants) were autopsied to determine pregnancy. The probability of settlement and pregnancy were compared for the different categories of females by mixed logistic models (Littell et al. 2006). Logistic models were also used to test differences in probabilities between settlement inside and outside SDHR and resident home ranges for colonisers and immigrants respectively. In order to investigate whether there were tendencies for aggregation of individuals, we measured the distances from (1) the coloniser's home range centre to the nearest SDHR centre and (2) the immigrant's home range centre to the nearest resident home range centre. These observed nearest neighbour distances were compared to the expectations from random dispersion.

The strength of this experimental field study was that it was sufficiently replicated in time. However, the weakness was that it lacked spatial replication and was thus, strictly speaking, only valid at the spatial scale and for the kind of habitats available on this one island.

3.2. Paper II

In this paper a field experiment was conducted in a large experimental area at Evenstad research station, south-east Norway. In comparison to paper I, in which the field experiment was conducted on one patch only, this experiment constituted 24 patches differing in habitat quality (high/low) and avian predation risk (open/closed). The experiment was replicated in two seasons. In each replicate, 2 founder demes were introduced at each end of the 300 meter long (100 m wide) experimental area. Each of the 4 demes constituted three mothers and their litters. Individuals were then allowed to colonise all empty patches at increasing distance from the release patch. The individuals were monitored by live traps. At the level of individual animals, we estimated colonisation probability with logistic regression and colonisation distance with linear regression. At the patch level, the number of individuals per patch (i.e. deme size) was analysed with log-linear models. We focused on deme size at two moments in the experimental season. The first moment was just after the major colonisation event in the founder animals was completed, and before the recruitment of new cohorts. At this moment we could highlight how experimental factors (colonisation distance, patch quality and predation risk) affected deme size through the colonisation process. The second analysis was conducted on the final deme sizes in the autumn. At this final stage in the season we could highlight to what extent the experimental factors (including their effect on the colonisation processes and local demographic processes) had affected deme size just before the onset of the winter. Details on the exact experimental setup and the way of manipulating distance, predation and habitat quality are given in paper II.

Two weaknesses of this particular experimental setup were that we did not monitor the true predation pressure (i.e. kill rates) or sample detailed vegetation data which could have strengthened our inference of the results. The strength of the experiment was that the spatial scale was considerably larger than what has commonly been used in previous enclosure experiments addressing dispersal.

3.3. Paper III

In this paper we monitored a riparian metapopulation of root voles constituting 15 islands and the mainland, in the largest river (Glomma) in Norway. Individuals were captured by live trapping during 13 sessions over 4 years to sample island specific detection histories. This approach allowed us to estimate the occupancy dynamics (i.e. the probabilities of initial occupancy, colonisation and extinction) while at the same time, accounting for the possibility of false absence (MacKenzie et al. 2002, MacKenzie et al. 2003). Occupancy dynamics and the covariate impacts of island geometry, habitat quality, river dynamics and population size (island and mainland) were estimated with the programme PRESENCE 4.3. (Hines 2006). Island geometry was sampled by Global Positioning System (GPS) plots and implemented in Arc GIS 9.3 for the calculation of island area and distance to the nearest neighbouring island and to the mainland. Habitat quality was sampled as the proportional cover of different plant species at every trap location. River dynamics (meters above sea level) were recorded at a downstream gauging station. Statistical analyses were conducted in two stages. In the first stage covariates with a strong impact on the rate parameters (initial occupancy, colonisation, extinction and detection) were identified in univariate models. In the second stage those covariates with a strong impact in univariate models were added in all combinations to identify the most parsimonious model of the occupancy dynamics. We used AIC, ΔAIC, and AIC weights for selecting the best model for inference of covariate impact (Buckland et al. 1997).

A challenge to this study was that the monitoring schedule could not be exactly planned, but was dependent on the current water level due to safety precautions. This caused some variation in the number of sessions conducted each year. The major strength of this study was that each island represented a clearly distinct habitat patch in a natural system. This allowed for identification of the most influential covariates of the probability of colonisation and of the probability of extinction in a cyclic vole metapopulation.

3.4. Paper IV

This paper is based on knowledge gathered over nearly 20 years of experimental research conducted at Evenstad Research Station. We, as probably most reviewers, were challenged by the large amount of other relevant studies with sometimes contradicting results. Our paper is therefore close to what is commonly referred to as an opinion paper in peer-reviewed scientific journals. The literature cited is

unavoidably biased towards papers and books that are in line with the presented view on vole

population cycles. However, we feel it is justified to state that opposing views are taken into account.

In addition, the paper ends with testable predictions that could be used by any researcher to refute (or

strengthen) our view.

4. Results and discussion

4.1. Colonisation in the increase phase

Paper II confirmed our prediction that the majority of first cohort individuals disperse from high density source demes when empty habitat patches exist in the neighbourhood (Andreassen and Ims 2001). In paper I we found no indications that dispersing female bank voles used the presence of conspecific cues as determinants of settlement. Female colonisers settled independently of our simulated deserted home ranges and immigrants settled both inside and outside resident home ranges. A previous methodological study to assess different statistical models accounting for spatial autocorrelation using the same dataset, found that habitat selection was based on variables representing cover and food (Keitt et al. 2002). In paper II we found similar patterns: the colonising root voles were uniformly distributed on the same quality habitats and post-colonisation deme sizes were larger in the high quality habitats than in the low quality habitats. The importance of high quality habitats in the settlement decision of colonising voles was also confirmed in the island occupancy study reported in paper III. The probability of colonisation was highest on islands with the highest proportion of food and cover vegetation.

The uniform post-colonisation deme size distribution in root voles (paper II) is in line with previous experimental studies that have shown that dispersal processes are density dependent and contribute to the regulation of spatial population dynamics (Aars and Ims 2000, Andreassen and Ims 2001, Gundersen et al. 2002). Paper II enhances our understanding of the previous studies by showing that such spatial regulation can act on spatial scales larger than that usually employed in experimental studies of small rodents. Such a social regulation of individual space use, with effects on population level dispersion, was also evident in bank voles as colonisers tended to have a higher probability of settlement than immigrants (paper I). We suspect that this difference was due to the rejection of the whole experimental plot (island) in the settlement decision of immigrant female bank voles (Ims 1989 and paper I). Immigrant females that settled on the island had a lower probability of pregnancy than colonisers, and those immigrants that settled within the home range of residents had a nearly zero probability of pregnancy, indicating rejection from high quality habitat as well as reproductive suppression by resident females (Mappes et al. 1995, Koskela et al. 1997, Jonsson et al. 2002). In addition, immigrant female home ranges were larger than residents' indicating settlement in lower quality habitats (Ims 1987 and paper I). Both of the species investigated (paper I-III), aggregated

in habitats of the highest quality, which will likely act to intensify social interactions even though the overall population density was low (McGuire and Getz 1998, sensu Greene and Stamps 2001). Our results provide evidence supporting the presence of social fences around high quality habitats at low population density. Hence, in the increase phase voles seem to actively search out vacant habitats and settle in them, conditional on habitat quality and population density.

In paper II we found no effect of distance from source patches on post-colonisation deme sizes despite employing a much larger scale than what is common in enclosure studies on voles. We also note that none of the measurements of isolation were related to the probability of colonisation in paper III, despite the extreme matrix composition (strong currents in the river) in this observational study. In paper II we also found no effect of predation on post-colonisation deme sizes. The first born cohort individuals, emigrating in early summer, demonstrated the large capacity of voles for colonising spatially scattered habitats (sensu Stenseth and Ims 1993a) – a capacity that explains the fast reclaiming of empty habitat space following crashes in cyclic populations. When the predation pressure is low, the cost of the transient stage of the colonisation process (*sensu* Ims and Yoccoz 1997) appears to be low for such a mobile species as the root vole (Steen 1995). This implies that in the increase phase of the small rodent cycle, when the predation pressure is indeed very low (Ims and Andreassen 2000) and there is lots of vacant space, habitat selection at the scale of patchy populations (*sensu* Hanski 1999) is not likely to be constrained by such costs.

4.2. Colonisation and extinction in population cycles

In paper III we investigated, by means of occupancy modelling, the influence of different covariates on root vole colonisation and extinction on 15 islands over 4 years. In our study the number of colonisation events was similar to the number of extinction events. This supports the equilibrium theory of balance between colonisation and extinction given presence of source populations (MacArthur and Wilson 1967, *sensu* Hanski 1999). However, our results show that covariates other than island (patch) area and isolation are needed to best predict patch occupancy dynamics. Similarly to a number of other studies, we found that habitat quality, and not any measurement of island geometry, had the strongest impact on the probability of colonisation (e.g. Franken and Hik 2004, Robles and Ciudad 2012). It is possible, however, that individuals encountered some islands more

frequently just because they were larger or closer to the point of emigration (Gustafson and Gardner 1996). However, the strong preference for optimal habitats probably caused rejection of islands with low proportions of cover and food irrespective of island size (Ims et al. 1993, Andreassen et al. 1998, see also paper I and II). This apparently happened despite rejection of an island requiring the individual to enter the water again in search for better habitats (see also paper I). In species with a strong preference for particular habitats, a high dispersal capacity may counteract isolation. If individuals have the capacity to easily prospect all habitat patches within a metapopulation, distance between habitat fragments is obviously less important than habitat quality (Robles and Ciudad 2012). *Microtus* species are considered to have evolved such high dispersal capacity (Ebenhard 1990), which may to a large extent counteract isolation. In line with the results from paper II, we did not find any impact of distance on the probability of colonisation. However, the probability of colonisation was influenced by the population density on the mainland the previous session. Apparently, the flow of individuals entering the water from the mainland was much more important than the degree of isolation on the probability of colonisation. Similar correlations are found between mainland numbers and island numbers in previous studies of small mammals (Hanski and Peltonen 1988, Peltonen and Hanski 1991). Hence the study system could be characterised as a source-sink or a mainland-island metapopulation (Harrison 1991, Hanski 1999)(cf. Harrison 1991, Hanski 1999) .

The descriptors of island geometry had little impact on the probability of extinction compared to population size and maximum water level. Other studies have also found that patch area may not be an appropriate surrogate of population size (Pellet et al. 2007, Franzen and Nilsson 2010). In addition, our results confirm that dynamic features of the landscape, representing spatially correlated environmental stochastcity, may influence extinction substantially (Snall et al. 2005). We assume inundation of islands to be the causal factor relating high water levels and extinction. However, owing to high capacities for dispersal and habitat tracking, voles can rapidly colonise high quality habitat patches that have previously gone extinct, due to demographic (small population size) and environmental (e.g. extreme climate events) stochasticity, across the entire landscape.

Box 1. Bank vole occupancy on the islands in river Glomma

Prior to the island study reported in paper III nothing was known about the presence of small rodents on the islands. The extensive trapping (54 surveys divided across 13 seasons) revealed that bank voles were abundant in some seasons on some of the islands. Using the same approach as for the root vole detection histories, we aimed to investigate the bank vole occupancy dynamics (see methods in paper III). However, bank voles were present on only 5 of the islands. The raw detection history data indicated 7 colonisation events and 6 extinctions on these 5 islands. Modelling of the occupancy dynamics with all rate parameters held constant showed that the probability of occupancy in the first season (ψ_0) was 0.16 ($\pm$ 0.15 SE), the probability of colonisation (γ) was only 0.05 ($\pm$ 0.02 SE) and the probability of extinction (ε) was 0.26 ($\pm$ 0.09 SE) when accounting for a detection probability estimated as 0.62 ($\pm$ 0.05 SE). Consequently, occupancy in bank voles was much more restricted and stable than in root voles (see paper III). Because colonisation and extinction were rare events, the detection history of bank voles was not suitable for investigation of covariate impact on multi-season occupancy dynamics. However, some interesting aspects of the differences between bank voles and root vole dynamics could be derived from the data. Calculations of the population growth rates ($r_t = \ln(N_{t+1}/N_t)$ for the summarised number of captured individuals on the islands and on the mainland, showed that the bank vole growth rates on the islands were strongly correlated to the mainland growth rates (linear regression; $r^2 = 0.68$, $F_{1,10} = 22.03$, $P < 0.001$; Fig. 1A). By contrast, the root vole growth rates on the islands were not correlated to the growth rates on the mainland ($r^2 = 0.01$, $F_{1,10} = 0.10$, $P = 0.76$). This may be expected since the probability of root vole colonisation of islands (paper III) was related to the number of individuals on the mainland in the previous season (t -1). Thus, correlating the growth rate the previous season (t-1) on the main land with the growth rates on the islands (t) confirmed the dependence in root voles of colonisers from the mainland, as these growth rates were highly correlated ($r^2 = 0.57$, $F_{1,9} = 11.89$, $P = 0.007$; Fig. 1B). In contrast, the bank vole growth rates on the islands were not correlated with the population growth rates on the mainland the previous season ($r^2 = 0.07$, $F_{1,9} = 0.06$, $P = 0.81$).

Box 1 – continued

These results indicate that the bank vole population dynamics on the islands are synchronous with the mainland, despite not being connected by dispersal (i.e. the probability of colonisation was very low). Root voles on the islands, on the other hand, lagged one season behind in their dynamics and depended strongly on colonisers from the mainland (i.e. the probability of colonisation was related to population size on the mainland the previous season, paper III). All 5 islands with bank vole populations had large perimeters (mean ± SE: 752 ± 148 m) compared to the island without bank voles (161 ± 38 m). In addition, all these 5 islands had large trees present. Only one island without bank voles had large trees, but this island had nearly no field layer vegetation (20%), and was not preferred by root voles either (one individual in 2 of the surveys). Bank voles were rarely extirpated from these islands with trees, while root voles commonly went extinct after high flood levels (paper III). Maybe this difference is related to the ability of bank voles to climb trees, aiding survival of individuals during floods, while ground bounded root voles may be more likely to be flushed away by strong currents during inundation.
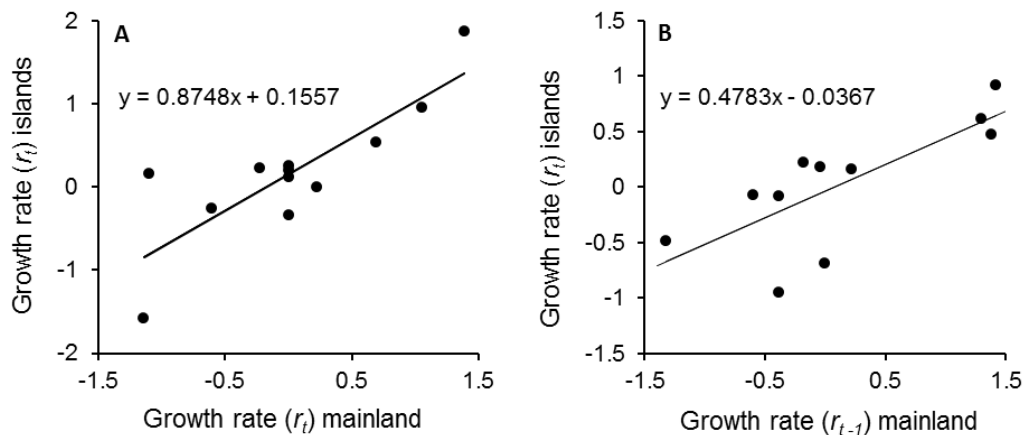
Figure 1. (A) The relationship between bank vole growth rates on the islands (t) and on the mainland (t). (B) The relationship between root vole growth rates (t) on the islands and on the mainland the previous session (t-1).

Note: A few other species of small mammals were also captured on the islands. On two of the islands we captured *Mustela nivalis*, a well-known predator of small rodents (Klemola et al. 1997). On three islands we captured *Apodemus* spp. and on 4 islands we captured *Sorex* spp and a few *Neomys fodiens*.

Inevitably interspecific studies are prone to produce species-specific results and inferences. Some additional data on the much less common bank vole in the focal island-mainland system (not presented in Paper III) can be used here to illustrate this (see Box 1). Evidently the two species differ in their patch occupancy dynamics, probably due to their adaptations to different habitats and landscape heterogeneity. Root vole colonisation of these islands is best characterised by high colonisation capacity and habitat tracking (paper III). In the context of the specific study system, it is important to note that root voles often live in close connection to wetlands and water systems and are good swimmers (Tast 1966, Pokki 1981). The important role of habitat selection and high colonisation capacity in the increase phase of root vole metapopulations was also evident in paper II. This indicates that root voles are more vulnerable to loss of high quality source habitats (i.e. populations surviving the low phase) than by fragmentation *per se*. Bank vole occupancy on the islands was restricted to 5 islands and the probabilities of colonisation and extinction were low (Box 1). Bank voles prefer drier patches in a wider range of forest habitats and open areas (Myllymaki 1977). Because of their adaptation to a wider range of habitats, bank voles may be more resilient to changes in habitat quality (Box 1), while they may be less resilient to an increasing degree of isolation of habitats. In summary, the result presented in paper III and Box1 may indicate that root voles are adapted to very patchy habitats and depend on only a few high quality source patches to build up spatially extensive, peak phase metapopulations (and thus cyclic dynamics), while bank voles are less adapted to patchiness and depend more on high connectivity (or more continuous habitats) to show cyclic dynamics (Dalkvist et al. 2011).

An important methodological issue regarding metapopulation studies of small mammals arose in paper III; the importance of accounting for imperfect detection to achieve unbiased estimates of occupancy dynamics. Although we used live traps with capture probabilities close to 100% in enclosure studies on root voles (Aars et al. 1999, paper II), the average detection probability was only 70% in our field study of the riparian root vole island-mainland metapopulation. The detection probability varied with week of the year and size of the island, probably reflecting population size. This partly confirms that most zeros recorded in time series on vole abundance (the trap density is normally low in such studies) may just reflect densities below some threshold at which voles are extremely hard to capture. Accounting for the possibility of pseudo-extinctions may not be detrimental to inferences based on long-term time series analyses of viable vole populations. However, underrating

metapopulation persistence may have serious consequences for management and conservation of more extinction prone species. In our study, detection peaked in the middle of summer. At this time of year detection probability was close to 90 % on the larger islands. In comparison, the average detection probability of bank voles was only 62 % (Box 1). This shows that detection probability may also vary between species and that identification of species-specific covariates of the spatio-temporal variation in detection probability is necessary to achieve reliable estimates of occupancy dynamics (Tanadini and Schmidt 2011).

4.3 New views on vole population cycles

The increase phase of cyclic vole and lemming populations in the highly seasonal environment of boreal and arctic regions is initiated from local demes in the spring that have persisted through the crash phase winter. We claim that population growth in the subsequent increase phase of the cycle is enhanced by a high degree of space sharing (sociality) among reproductive females (Ostfeld 1985, Ylonen et al. 1988, Jonsson et al. 2002). Such space sharing may be induced by habitat patchiness and even enforced by heterogeneous snow conditions in winter (Aars and Ims 2002, Korslund and Steen 2006, Reid et al. 2012). These social females have a high reproductive output due to good resource conditions (Rémy 2011) and benefit from communal breeding (Andreassen et al. 1990, Hayes 2000), social thermoregulation (Hayes 2000, Gilbert et al. 2010) and shared protection against infanticidal intruders (Wolff 1993, Ylonen et al. 1997, Wolff and Peterson 1998). Our studies also show that the dispersal rate is high during the increase phase (paper II). This is due to generally low densities (iversely density dependent dispersal: Andreassen and Ims 2001). Because a lot of vacant habitat exists at this stage, dispersal leads to colonisation of previously empty habitat patches rather than intrusion of immigrants into established social groups (paper I). The large capacity of root voles for rapid colonisation through high mobility and active searching for vacant patches is demonstrated in paper II.

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). This inverse density dependence is, at least partly, due to immigration becoming limited by social fences (Hestbeck 1982, Gundersen et al. 2001) as the landscape gets saturated (e.g. Bondrup-Nielsen and Ims 1988b, see also paper I)

We suggest that the crash phase of vole population cycles is initiated by increased predation, resulting from predator numerical and functional responses (e.g. Sundell 2006). Our experimental studies on root voles have shown that the turnover of dominant males from social groups due to natural or experimentally simulated 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, see details about each step in the disruption of the social system and the negativ effect on population growth rate in paper IV). The negative population growth may be further exacerbated by inversely density dependent dispersal (Andreassen and Ims 2001) because of the generally high predation pressure on transient individuals in the crash phase (Ims and Andreassen 2000).

As previously predicted, we expect that the extended period of low density is caused by continued high predation rates (Boonstra et al. 1998). Thus, 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). Based on our experimental studies, inverse density dependent dispersal is also prominent in this phase of the cycle, with a high proportion of individuals dispersing in attempts to colonise newly vacant high quality habitat.

We emphasise the important role of dispersal in all phases of the cycle, similar to what we propose in the case of social organisation. Both dispersal and sociality may confer opposing demographic effects in the increase and crash phases of the cycle. At low density, in the increase phase, the high proportion of dispersing animals gives a rapid colonisation of vacant habitat patches, which contributes to rapid population growth (paper II). At this stage even long-distance dispersal across hostile matrix habitat is likely to end up in successful colonisation of vacant patches (paper II-III). 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 then high which thus contributes further to the decline of the population (Ims and Andreassen 2000, Andreassen and Ims 2001).

Note that we do not claim that intrinsic mechanisms, either alone or 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. Still we 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. Specifically we suggest that different innate propensities for sociality and dispersal among different rodent species may be related to inter-specific variation in topology of the cycles (i.e. cycle shape and amplitude; Turchin et al. 2000) and degree of spatial population synchrony (details are given in Paper IV).

5. Concluding remarks

Concerning the major aim of this thesis to elucidate the role of colonisation in cyclic vole (meta)populations, our results show that spatially scattered (sub)populations that have survived the crash phase are able (under otherwise benign conditions) to provide colonists even to remote habitat patches imbedded in hostile matrix and thus pave the way to a new increase and peak phase. Owing to high capacities for dispersal and habitat tracking, voles can rapidly colonise high quality habitat patches that have previously gone extinct across the entire landscape. We have also given our views on how sociality and dispersal behaviour facilitate a sufficiently high number of emigrants to overcome negative effects of isolation and predation.

However, even though vole metapopulations persist through normal cyclic low phases, the likelihood of metapopulation persistence may dramatically change if source populations no longer peak due to habitat degradation (in this thesis exemplified by the root voles) or if habitat fragmentation causes extreme matrix conditions (exemplified by the bank voles). Degraded snow cover properties during winters have been shown to prevent the build-up of cyclic peak phases (Ims et al. 2008, Kausrud et al. 2008). Ice and snow crust formations close to the ground limit space and access to food (Korslund and Steen 2006, Reid et al. 2012) and may have devastating effects on survival and reproduction and thus eliminate the source for population growth in time and space. (Aars and Ims 2002, Ims et al. 2011). In light of the dampened and/or collapsed cycles in boreal and arctic regions in recent years (Henden et al. 2009, Elmhagen et al. 2011) that is suspected to result from climate change (Ims et al. 2008, Kausrud et al. 2008), knowledge about the conditions and processes required for the recovery phase after population lows becomes essential. If populations are no longer able to recover from crashes and experience sustained periods with small populations scattered on isolated patches in the landscape, there is even a risk of metapopulation extinction. Such a situation may have recently taken place in the grey-sided vole (*Myodes rufocanus*) in the forested lowlands of northern Sweden (Ecke et al. 2010).

Either the extinction of rodent metapopulations or the loss of their cyclic peaks will have profound impacts on the ecosystem in which the small rodent species are regularly abundant and maintain keystone roles in the food web.

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Evenstad, September 2012   Petter Glorvigen

7. References

Aars, J. and Ims, R. A. 2000. Population dynamic and genetic consequences of spatial density-dependent dispersal in patchy populations. – Am. Nat. 155: 252–265.

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

Aars, J. et al. 1995. Root voles - litter sex-ratio variation in fragmented habitat. – J. Anim. Ecol. 64: 459–472.

Aars, J. et al. 1999. Demographic consequences of movements in subdivided root vole populations. – Oikos 85: 204–216.

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

Allee, W. C. 1951. The social life of animals. – Beacon Press.

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. 1985. The role of nutrition in population cycles of microtine rodents. – Acta Zool. Fenn. 173: 13–17.

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

Begon, M. et al. 2006. Abundance. – In: Begon, M., Townsend, C. R., and Harper, J. L. (eds.), Ecology: From individuals to ecosystems. Blackwell Publishing, pp. 410–438.

Bjørnstad, O. N. et al. 1995. Geographic gradient in small rodent density-fluctuations - a statistical

    modeling approach. – Proc. R. Soc. B 262: 127–133.

Bjørnstad, O. N. et al. 1998. Effects of habitat patchiness and connectivity on the spatial ecology of the

    root vole Microtus oeconomus. – J. Anim. Ecol. 67: 127–140.

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. Demography during a population crash of the wood

    lemming, *Myopus-schisticolor*. – Can. J. Zool. 66: 2442–2448.

Bondrup-Nielsen, S. and Ims, R. A. 1988b. Predicting stable and cyclic populations of *Clethrionomys*.

    – Oikos 52: 178–185.

Bonte, D. et al. 2012. Costs of dispersal. – Biol. Rev. 87: 290-312.

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

    219.

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. 2006. Population limitation of the northern red-backed vole in the boreal

    forests of northern Canada. – J. Anim. Ecol. 75: 1269–1284.

Boonstra, R. and Krebs, C. J. 2012. Population dynamics of red-backed voles (*Myodes*) in North

    America. – Oecologia 168: 601–620.

Boonstra, R. et al. 1998. Population cycles in small mammals: The problem of explaining the low

    phase. – Ecology 79: 1479–1488.

Boutin, S. 1990. Food supplemantation experiments with terrestrial vertebrates - patterns, problems,

    and the future. – Can. J. Zool. 68: 203–220.

Bowler, D. E. and Benton, T. G. 2005. Causes and consequences of animal dispersal strategies:

    relating individual behaviour to spatial dynamics. – Biol. Rev. 80: 205–225.

Brashares, J. S. et al. 2010. Social 'meltdown' in the demise of an island endemic: Allee effects and

    the Vancouver Island marmot. – J. Anim. Ecol. 79: 965–973.

Brown, J. H. and Kodric-Brown, A. 1977. Turnover rates in insular biogeography - effect of immigration

    on extinction. – Ecology 58: 445–449.

Buckland, S. T. et al. 1997. Model selection: An integral part of inference. – Biometrics 53: 603–618.

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. 1952. Mortaltiy amon voles (*Microtus agrestis*) at Lake Vyrnwy, Montgomeryshire, in 1936-1939. – Phil. Trans. R. Soc. B 263: 505–552.

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.

Clobert, J. et al. 2001. Dispersal. – Oxford Univ. Press.

Courchamp, F. et al. 2008. Allee Effects in Ecology and Conservation. – Oxford Univ. Press.

Dalkvist, T. et al. 2011. How Predation and Landscape Fragmentation Affect Vole Population Dynamics. – PLoS One 6: doi: 10.1371/journal.pone.0022834.

Danchin, E. et al. 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. – Ecology 79: 2415–2428.

Ebenhard, T. 1990. A colonization strategy in field voles (*Microtus-agrestis*): reproductive traits and body size. – Ecology 71: 1833–1848.

Ecke, F. et al. 2010. Landscape structure and the long-term decline of cyclic grey-sided voles in Fennoscandia. – Landsc. Ecol. 25: 551–560.

Elmhagen, B. et al. 2011. Changes in vole and lemming fluctuations in northern Sweden 1960-2008 revealed by fox dynamics. – Ann. Zool. Fenn. 48: 167–179.

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.

Ergon, T. et al. 2011. Delayed density-dependent onset of spring reproduction in a fluctuating population of field voles. – Oikos 120: 934–940.

Franken, R. J. and Hik, D. S. 2004. Influence of habitat quality, patch size and connectivity on colonization and extinction dynamics of collared pikas *Ochotona collaris*. – J. Anim. Ecol. 73: 889–896.

Frankham, R. 2005. Genetics and extinction. – Biol. Conserv. 126: 131–140.

Franzen, M. and Nilsson, S. G. 2010. Both population size and patch quality affect local extinctions and colonizations. – Proc. R. Soc. B 277: 79–85.

Fretwell, S. D. and Lucas, H. L. 1970. On territorial behaviour and other factors influencing habitat distributions in birds. – Acta Biotheoretica 19: 16–36.

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.

Gorini, L. et al. 2011. Guild composition and habitat use of voles in 2 forest landscapes in south-eastern Norway. – Integr. Zool. 6: 299–310.

Graham, I. M. and Lambin, X. 2002. The impact of weasel predation on cyclic field-vole survival: the specialist predator hypothesis contradicted. – J. Anim. Ecol. 71: 946–956.

Greene, C. M. and Stamps, J. A. 2001. Habitat selection at low population densities. – Ecology 82: 2091–2100.

Gundersen, G. and Andreassen, H. P. 1998. Causes and consequences of natal dispersal in root voles, *Microtus oeconomus*. – Anim. Behav. 56: 1355–1366.

Gundersen, G. et al. 2002. Individual and population level determinants of immigration success on local habitat patches: an experimental approach. – Ecol. Lett. 5: 294–301.

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

Gundersen, G. et al. 1999. Intersexual attraction in natal dispersing root voles *Microtus oeconomus*. – Acta Theriol. 44: 283–290.

Gustafson, E. J. and Gardner, R. H. 1996. The effect of landscape heterogeneity on the probability of patch colonization. – Ecology 77: 94–107.

Hanski, I. 1999. Metapopulation ecology. – Oxford Univ. Press.

Hanski, I. and Peltonen, A. 1988. Island colonization and peninsulas. – Oikos 51: 105–106.

Hanski, I. and Gilpin, M. 1991. Metapopulation dynamics - brief history and conceptual domanin. – Biol. J. Linnean Soc. 42: 3–16.

Hanski, I. et al. 1991. Specialist predators, generalist predators, and the microtine rodent cycle. – J. Anim. Ecol. 60: 353–367.

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. 1985. *Clethrionomys* food - generic, specific and regional characteristics. – Ann. Zool. Fenn. 22: 315–318.

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.

Hansson, L. and Henttonen, H. 1988. Rodent dynamics as community processes. – Trends Ecol. Evol. 3: 195–200.

Hansteen, T. L. et al. 1997. Effects of spatiotemporal scale on autocorrelation and home range estimators. – J. Wildl. Manage. 61: 280–290.

Harrison, S. 1991. Local extinction in a metapopulation context - an empirical evaluation. – Biol. J. Linnean Soc. 42: 73–88.

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.

Henden, J. A. et al. 2009. Nonstationary spatio-temporal small rodent dynamics: evidence from long-term Norwegian fox bounty data. – J. Anim. Ecol. 78: 636–645.

Henden, J. A. et al. 2011. Population dynamics of tundra voles in relation to configuration of willow thickets in southern arctic tundra. – Polar Biol. 34: 533–540.

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

Hildén, O. 1965. Habitat selection in birds: a review. – Ann. Zool. Fenn. 2: 53–75.

Hines, J. E. 2006. PRESENCE - Software to estimate patch occupancy and related parameters. USGS-PWRC.

Hovland, N. et al. 1999. Foraging behaviour of the root vole *Microtus oeconomus* in fragmented habitats. – Oecologia 121: 236–244.

Huitu, O. et al. 2005. Spatial synchrony in vole population fluctuations - a field experiment. – Oikos 109: 583–593.

Ims, R. A. 1987. 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. 1989. Kinship and origin effects on dispersal and space sharing in *Clethrionomys-rufocanus*. – Ecology 70: 607–616.

Ims, R. A. 1997. Determinants of geographic variation in growth and reproductive traits in the root vole. – Ecology 78: 461–470.

Ims, R. A. and Yoccoz, N. G. 1997. The study of transfer processes in metapopulations: emigration, dispersal and colonization. – In: Hanski, I. and Gilpin, M. E. (eds.), Metapopulation Dynamics: Ecology, Genetics and Evolution. Academic Press, pp. 247–265.

Ims, R. A. and Andreassen, H. P. 1999. Effects of experimental habitat fragmentation and connectivity on root vole demography. – J. Anim. Ecol. 68: 839–852.

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 Fuglei, E. 2005. Trophic interaction cycles in tundra ecosystems and the impact of climate change. – Bioscience 55: 311–322.

Ims, R. A. et al. 1993. Predicting space use responses to habitat fragmentation - can voles *Microtus-oeconomus* serve as an experimental-model system (EMS) for capercaillie grouse *Tetrao-urogallus* in boreal forest. – Biol. Conserv. 63: 261–268.

Ims, R. A. et al. 2008. Collapsing population cycles. – Trends Ecol. Evol. 23: 79–86.

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

Inchausti, P. and Ginzburg, L. R. 2009. Maternal effects mechanism of population cycling: a formidable competitor to the traditional predator-prey view. – Phil. Trans. R. Soc. B 364: 1117–1124.

Johannesen, E. and Ims, R. A. 1996. Modelling survival rates: Habitat fragmentation and destruction in root vole experimental populations. – Ecology 77: 1196–1209.

Johannesen, E. and Andreassen, H. P. 1998. Survival and reproduction of resident and immigrant female root voles (*Microtus oeconomus*). – Can. J. Zool. 76: 763–766.

Jonsson, P. et al. 2002. Determinants of reproductive success in voles: space use in relation to food and litter size manipulation. – Evol. Ecol. 16: 455–467.

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

Keith, L. B. 1990. Dynamics of snowshoe hare populations. – Current Mammal. 4: 119–195.

Keitt, T. H. et al. 2002. Accounting for spatial pattern when modeling organism-environment interactions. – Ecography 25: 616–625.

Klemola, T. et al. 1997. Small mustelid predation slows population growth of Microtus voles: A predator reduction experiment. – J. Anim. Ecol. 66: 607–614.

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. 2005. Vole cycles and predation in temperate and boreal zones of Europe. – J. Anim. Ecol. 74: 1150–1159.

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

Koskela, E. et al. 1997. Territorial behaviour and reproductive success of bank vole *Clethrionomys glareolus* females. – J. Anim. Ecol. 66: 341–349.

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. et al. 2001. What drives the 10-year cycle of snowshoe haves? – Bioscience 51: 25–35.

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

Krebs, C. J. et al. 1995. Impact of food and predation on the snowshoe hare cycle. – Science 269: 1112–1115.

Kuussaari, M. et al. 1998. Allee effect and population dynamics in the Glanville fritillary butterfly. – Oikos 82: 384–392.

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. 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.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. – Am. Nat. 142: 911–927.

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

Lidicker, W. Z. and Ostfeld, R. S. 1991. Extra large body size in California voles - causes and fitness consequences. – Oikos 61: 108–121.

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.

Littell, R. C. et al. 2006. SAS® for Mixed Models. 2nd edition. – SAS Institute Inc.

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

Löfgren, O. 1995. Spatial organization of cyclic Clethrionomys females - occupancy of all available space at peak densities. – Oikos 72: 29–35.

MacArthur, R. H. and Wilson, E. O. 1967. The theory of island biogeography. – Princeton Univ. Press.

MacKenzie, D. I. et al. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. – Ecology 84: 2200–2207.

MacKenzie, D. I. et al. 2002. Estimating site occupancy rates when detection probabilities are less than one. – Ecology 83: 2248–2255.

Mappes, T. et al. 1995. Higher reproductive success among kin groups of bank voles (*Clethrionomys-glareolus*). – Ecology 76: 1276–1282.

McGuire, B. and Getz, L. L. 1998. The nature and frequency of social interactions among free-living prairie voles (*Microtus ochrogaster*). – Behav. Ecol. Sociobiol. 43: 271–279.

McGuire, B. et al. 2009. Effects of conspecific and heterospecific residents on patterns of immigration in two species of voles. – Acta Theriol. 54: 321–332.

Molnar, P. K. et al. 2008. Modelling the mating system of polar bears: a mechanistic approach to the
Allee effect. – Proc. R. Soc. B 275: 217–226.

Morris, D. W. 2002. Measuring the Allee effect: Positive density dependence in small mammals. –
Ecology 83: 14–20.

Myllymaki, A. 1977. Interactions between field vole *Microtus agretsis* and its microtine competitors in
central Scandinavian populations. – Oikos 29: 570–580.

Oksanen, T. A. et al. 2001. Optimal allocation of reproductive effort: manipulation of offspring number
and size in the bank vole. – Proc. R. Soc. B 268: 661–666.

Oli, M. K. 2003a. Response to Korpimaki et al.: vole cycles and predation. – Trends Ecol. Evol. 18:
495–496.

Oli, M. K. 2003b. Population cycles of small rodents are caused by specialist predators: or are they? –
Trends Ecol. Evol. 18: 105–107.

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

Ostfeld, R. S. et al. 1993. Intrinsic density-dependent regulation of vole populations. – Nature 366:
259–261.

Ostfeld, R. S. et al. 1996. Of mice and mast. – Bioscience 46: 323–330.

Pellet, J. et al. 2007. An empirical evaluation of the area and isolation paradigm of metapopulation
dynamics. – Biol. Conserv. 136: 483–495.

Peltonen, A. and Hanski, I. 1991. Patterns of island occupancy explained by colonization and
extinction rates in shrews. – Ecology 72: 1698–1708.

Pokki, J. 1981. Distribution, demography and dispersal of the field vole, *Microtus agretis*, in the
Tvarminne archipelago, Finland. – Acta Zool. Fenn. 164: 1–48.

Ranta, E. et al. 1995. Synchrony in population dynamics. – Proc. R. Soc. B 262: 113–118.

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.

Robles, H. and Ciudad, C. 2012. Influence of habitat quality, population size, patch size, and connectivity on patch-occupancy dynamics of the middle spotted woodpecker. – Conserv. Biol. 26: 284–293.

Rosenzweig, M. L. 1981. A theory of habitat selection. – Ecology 62: 327–335.

Seldal, T. et al. 1994. Grazing-induced preteinase-inhibitors - a possible cause for lemming population-cycles. – Oikos 70: 3–11.

Selås, V. 1997. Cyclic population fluctuations of herbivores as an effect of cyclic seed cropping of plants: the mast depression hypothesis. – Oikos 80: 257–268.

Selås, V. 2006. Explaining bank vole cycles in southern Norway 1980-2004 from bilberry reports 1932-1977 and climate. – Oecologia 147: 625–631.

Sinclair, A. R. E. et al. 2003. Mammal population cycles: evidence for intrinsic differences during snowshoe hare cycles. – Can. J. Zool. 81: 216–220.

Snall, T. et al. 2005. Colonization-extinction dynamics of an epiphyte metapopulation in a dynamic landscape. – Ecology 86: 106–115.

Soininen, E. M. et al. 2009. Analysing diet of small herbivores: the efficiency of DNA barcoding coupled with high-throughput pyrosequencing for deciphering the composition of complex plant mixtures. – Front. Zool. 6: doi:10.1186/1742-9994-1186-1116.

Stamps, J. A. 1994. Territorial behavior - testing the assumptions. – Advances in the Study of Behavior, Vol 23. Academic Press Inc, pp. 173–232.

Stamps, J. A. 2001. Habitat selection by dispersers: integrating proximate and ultimate approaches. – In: Clobert, J., Danchin, E., Dhondt, A. A., and Nichols, J. D. (eds.), Dispersal. Oxford Univ. Press, pp. 230–242.

Steen, H. 1995. Untangling the causes of disappearance from a local population of root voles, *Microtus-oeconomus* - a test of the regional synchrony hypothesis. – Oikos 73: 65–72.

Steen, H. et al. 1996. Spatial and temporal patterns of small-rodent population dynamics at a regional scale. – Ecology 77: 2365–2372.

Steen, H. et al. 2005. Sheep grazing and rodent populations: evidence of negative interactions from a landscape scale experiment. – Oecologia 143: 357–364.

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. 1999. Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. – Oikos 87: 427–461.

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.), 1993a. The biology of lemmings. Academic Press.

Stenseth, N. C. and Ims, R. A. 1993b. Population dynamics of lemmings: temporal and spatial variation: an introduction. – In: Stenseth, N. C. and Ims, R. A. (eds.), The biology of lemmings. Academic Press, pp. 61–96.

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.

Stephens, P. A. et al. 1999. What is the Allee effect? – Oikos 87: 185–190.

Stephens, P. A. et al. 2002. Model complexity and population predictions. The alpine marmot as a case study. – J. Anim. Ecol. 71: 343–361.

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

Tanadini, L. G. and Schmidt, B. R. 2011. Population size influences amphibian detection probability: implications for biodiversity monitoring programs. – PLoS One 6: doi: 10.1371/journal.pone.0028244.

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

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

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

Ward, M. P. and Schlossberg, S. 2004. Conspecific attraction and the conservation of territorial songbirds. – Conserv. Biol. 18: 519–525.

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

Wiens, J. A. et al. 1993. Ecological mechanisms and landscape ecology. – Oikos 66: 369–380.

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

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. et al. 1988. Changing female spacing behavior and demography in an enclosed breeding population of *Clethrinoomys-glareolus*. – Holarctic Ecol. 11: 286–292.

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.

The experimental island in lake Kynnsjøen   (Photo: Petter Glorvigen)

Settlement in empty versus occupied habitats: an experimental study on bank voles

The experimental area at Evenstad research station   (Photo: Gry Gundersen)

The role of colonization in patchy population dynamics of a cyclic vole species

Glorvigen, P., Gundersen, G., Andreassen, H.P. Ims R.A.
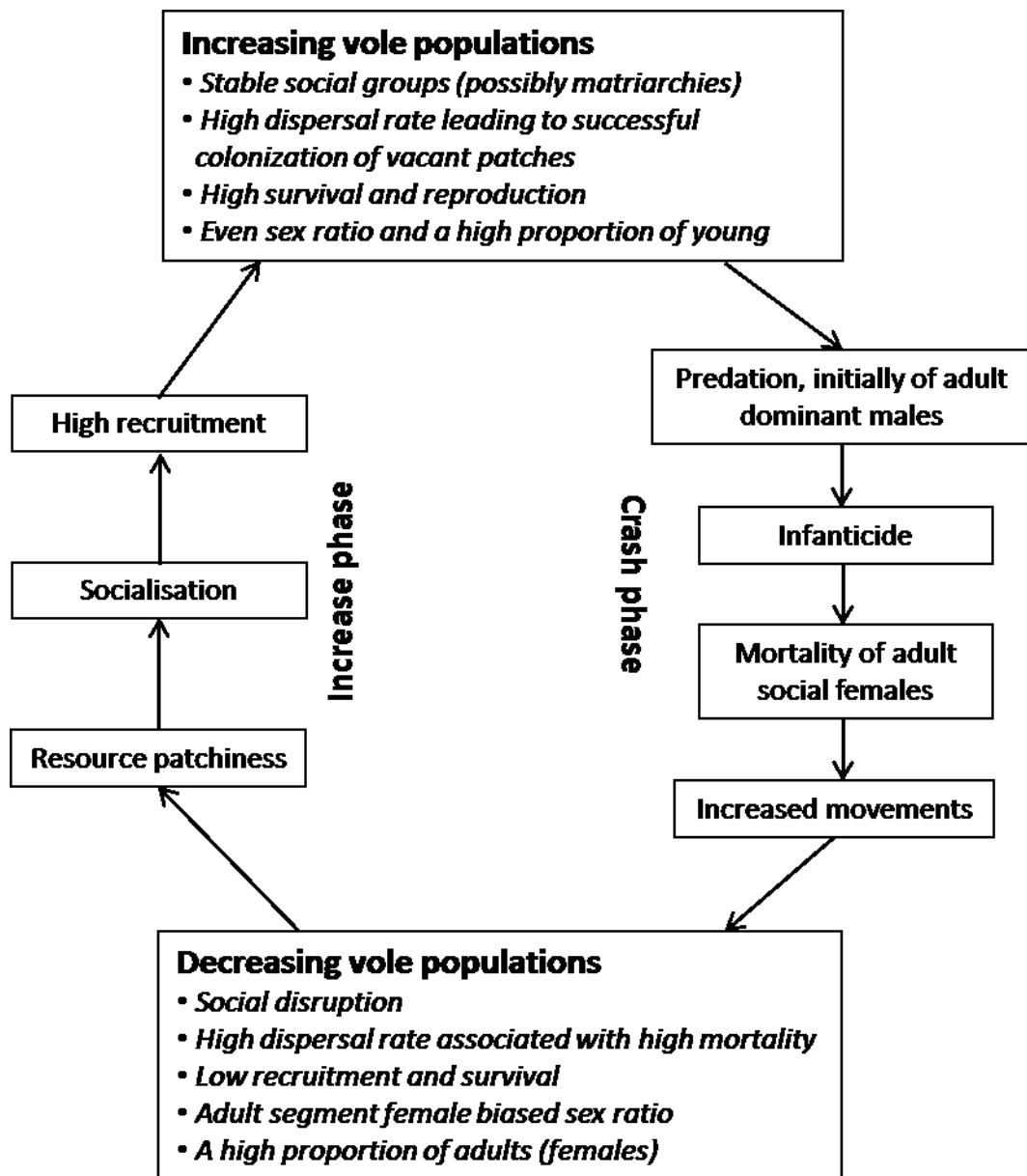
One of the studied islands in the river Glomma   (Photo: Petter Glorvigen)

Relative importance of habitat geometry, habitat quality, population size and environmental stochasticity on occupancy dynamics in a riparian mainland-island root vole metapopulation

Glorvigen, P., Andreassen, H.P. Ims R.A.

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*

High recruitment

Socialisation

Resource patchiness

Increase phase

Predation, initially of adult dominant males

Infanticide

Mortality of adult social females

Increased movements

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)*

Paper IV

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

Andreassen, H. P., Glorvigen, P., Rémy, A. and Ims, R.A.