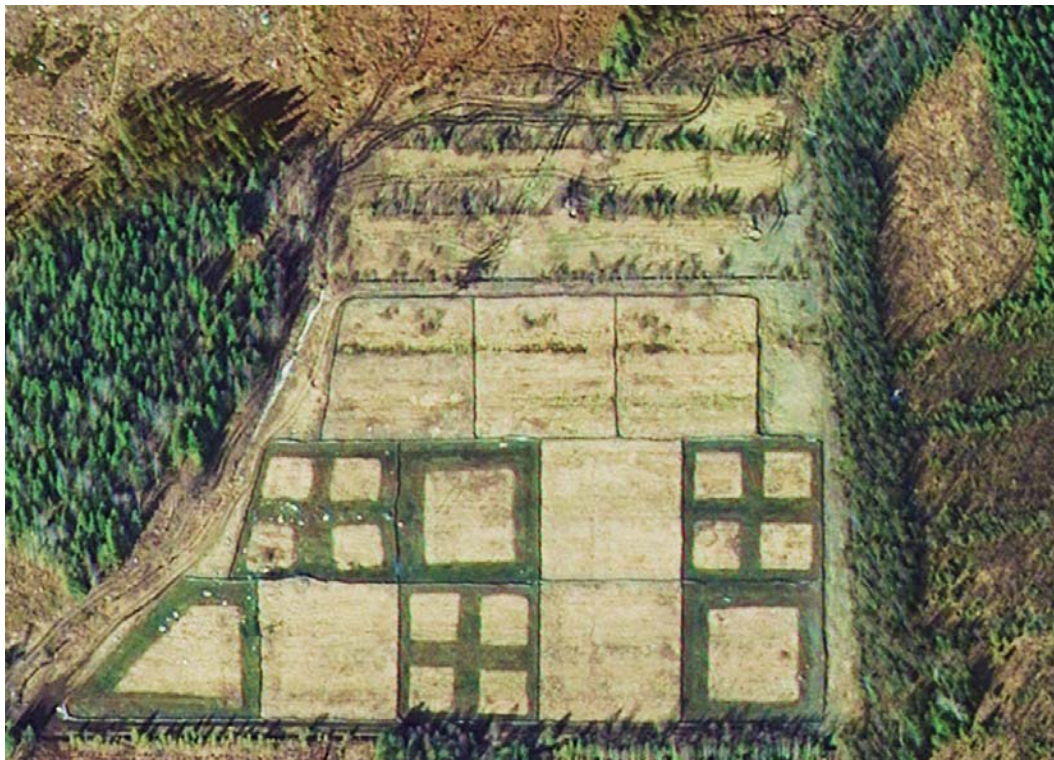


Marko Haapakoski

Habitat Fragmentation,
Seasonality and Predation
Affecting Behaviour and Survival
of Bank Voles *Myodes glareolus*



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Marko Haapakoski

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ABSTRACT

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Yhteenveto: Ympäristön pirstoutumisen, vuodenaikaisvaihtelun sekä petojen vaikutus metsämyyrän käyttäytymiseen ja hengissä selviytymiseen
Diss.

Habitat loss and fragmentation are the main causes for innumerable population and species having become threatened and for many of them already having gone extinct. Declines in species richness or populations are primarily caused by habitat loss, but habitat fragmentation, which subdivides populations into smaller units, is also important factor. Habitat fragmentation inevitably affects behaviour, space use and social interactions of individuals. These are likely to form essential part of the mechanism behind observed population declines. In this thesis I have studied the role of behaviour and space use of animals in fragmented landscape in a series of enclosure experiments. Summer experiments (I-III) concentrate more on behavioural effects of fragmentation whilst the winter experiments (IV-V) focus on behaviour, survival and onset of breeding with food supplementation and predation risk. I found that increased fragmentation led to increased risk-taking in the case of male bank voles and the hunting weasel when resources were distributed into separate patches. Female bank voles tended to stay inside the habitat patch and closer to their nest in more fragmented landscape. During winter snow evened out differences between habitat and matrix, but during spring when the breeding season starts, males in the fragmented treatment needed to take more risks by crossing the open matrix. Food in winter is important factor for the condition, survival and onset of breeding in bank voles. Surprisingly, also mere predation risk during winter had significant effect on vole population density, condition, survival and onset of breeding in the spring. To conclude, habitat fragmentation have direct survival and fitness consequences for individuals and it changes individual interactions, but direction of these effects depend on fragmentation types and duration and scale of experiments.

Keywords: Food supplementation; infanticide; least weasel; life history; reproduction; resource distribution; winter ecology.

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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the five original papers, which will be referred to in the text by their Roman numerals I-V.

I was involved in planning of the studies, conducted large part of the field work and was main writer in all articles I-V. I conducted all the statistical analysis in original papers I, II, IV and V, and jointly with AL in the original paper III.

- I Haapakoski, M. & Ylönen, H. 2010. Effect of fragmented breeding habitat and resource distribution on behaviour and survival of the bank vole (*Myodes glareolus*). *Population Ecology* 52: 427-435.
- II Haapakoski, M., Sundell, J. & Ylönen, H. 2012. Mammalian predator-prey interaction in a fragmented landscape: weasels and voles. Submitted manuscript.
- III Haapakoski, M., Vihervaara, H., Lensu, A., Sundell, J. & Ylönen, H. Infanticide effects on behavior of the bank vole (*Myodes glareolus*) in the fragmented habitat. Manuscript.
- IV Haapakoski, M. & Ylönen, H. 2012. Snow evens fragmentation effects and food determines overwintering success in ground dwelling voles. Submitted manuscript.
- V Haapakoski, M., Sundell, J. & Ylönen, H. 2012. Predation risk and food: opposite effects on overwintering survival and onset of breeding in a boreal rodent. *Journal of Animal Ecology* Published online, DOI: 10.1111/j.1365-2656.2012.02005.x

1 INTRODUCTION

The World is experiencing a major extinction crisis that is widely accepted among scientist (Stork 2010). It has been compared to five previous mass extinction events in geological history, when 65-95% of animals known from fossil records disappeared in each event (Raup 1986). Habitat loss and fragmentation are considered among the greatest contributors to recent and future extinctions and overall decreased biodiversity (Hanski 2005). Clearing habitats for agriculture and other human use are the main causes for habitat loss and fragmentation (MA 2005). The current biodiversity crisis, called as “the sixth mass extinction event wave” is still going on. Extinction dept (Tilman et al. 1994), the fact that there is time delay between destruction of habitat and disappearance of species, has thought to be the reason we have not seen an extinction wave sweeping species in full yet (Hanski 2005).

Climate is predicted to change at an increasing speed in the future and species may need to move to new areas or adapt to changing environmental conditions in their current range (Davis & Shaw 2001, Walther et al. 2002). Smaller gene pool in fragmented habitat might reduce the species ability to adapt to changing conditions and fragmentation might hinder the movements of individuals in to the new more suitable habitats. Climate change has been suggested to act together with the habitat loss and fragmentation and to speed up the extinction processes for the species currently in the extinction dept (Stork 2010). Therefore, the investigations of the habitat fragmentation effects and ways to mitigate those have become significant research field in ecology, conservation biology and landscape ecology (Lindenmayer & Fischer 2006).

Declines in species richness or populations are primarily caused by habitat loss, but habitat fragmentation, which subdivides populations in to smaller units, is also important factor in declining biological diversity (Hanski 2005). Habitat fragmentation can cause negative population trends for species in many ways (Primack 1998). Habitat fragmentation affects negatively to the stability and persistence of populations because isolation of remaining habitat patches increases the probability of extinction through demographic, environmental or genetic stochasticity (Lindenmayer & Fischer 2006). Habitat patchiness is

believed to affect almost all processes in population biology (Fahrig & Merriam 1994, Hanski and Gilpin 1997), especially movements, intra- and interspecific interactions, dispersal and colonization (Fahrig & Merriam 1994).

Majority of habitat fragmentation studies addresses the population level questions like patterns of species richness and abundance in fragmented habitat and between these patterns and landscape variables (reviewed by Debinski & Holt 2000, Fahrig 2003). The second major focus on fragmentation studies concentrate on mechanism behind observed patterns like the edge effect (Lahti 2001), population connectivity and genetic diversity (Gonzalez et al. 1998). Habitat fragmentation is suggested to change also predator - prey relationships but the directions and patterns of the change are unclear (Ryall & Fahrig 2006). The common prediction based on the review by Fahrig et al. (2003) is that the more specialized species, both in terms of habitat and food requirements, are suffering from habitat loss but habitat fragmentation effects *per se* are not clear (Fahrig 2003).

Short-term effects of habitat fragmentation on behaviour and social structure of individuals is of great importance (Ims et al. 1993, Bjornstad et al. 1998). We do not fully understand the precise individual and population level processes that determine species persistence or explains the observed population size declines in fragmented habitat (Banks et al. 2007). Life history parameters have been suggested to differ between continuous and fragmented habitat which may be important aspect to species' response to habitat fragmentation (Banks et al. 2007).

Microtine rodents have been successfully used as a model system for studying the effects of habitat fragmentation on behavioural and population scale studies (Ims & Andreassen 1999, Andreassen & Ims 2001). Compared to rare species and species less amenable for experimental manipulation, voles are relatively easy to work experimentally with. Results of studies conducted with voles have increased our knowledge about the effect of habitat fragmentation (Ims et al. 1993, Andreassen et al. 1996, Wolff et al. 1997) and have been extrapolated and applied, for example, in the case of forest fragmentation and space use in more difficultly studied larger vertebrate species, such as Capercaillie (*Tetrao urogallus*) in a study by Ims et al. (1993).

In my thesis, I have studied short-term effects of habitat fragmentation on behavior and fitness of bank voles in four experiments. More precisely I was manipulating resource availability, predator-prey interaction and infanticide by males with summer experiments (I-III). In winter experiments I was studying the food effect in fragmented habitats (IV). The last of my original publications (V) deals with fitness effects of predation risk and food during the non-breeding season in winter when the fragmentation effect disappears due to snow cover. The abundance and distribution of resources such as food for all individuals (Ims 1987, Ylönen & Viitala 1991), receptive females for males (Ims 1988) and safe refuges for the prey species (Johannesen et al. 2003) influence the space use and fitness of the individuals, but in which direction in fragmented landscape, is not known. Ryall & Fahrig (2006) give simple predictions of outcome of predator-prey interaction in fragmented landscape for each type of predators

(Table 1). Small isolated patches may provide a safe refuge from a specialist predator exploiting the same habitat, if specialist predator is exposed to same risks of top-avian predators when leaving the protective habitat (Ryall & Fahrig, 2006). The same may apply for protection against infanticidal conspecifics, which often behave similarly as special predators like small mustelids, albeit targeting on vulnerable nestlings instead of adult prey. Habitat fragmentation and formation of small isolated patches, nevertheless suitable for one or few individuals to reproduce, may be beneficial for survival and may even have positive effects on population dynamics in small mammals.

TABLE 1 Summary of assumptions regarding biology of predators in fragmented habitat in theoretical papers modified from Ryall & Fahrig (2006).

Predator type	No. studies	Feeding strategy	Habitat use/restrictions	Effect of prey on predator populations	Effect of predator on prey populations
Specialist	7	One prey species	Restricted to same habitat as prey species	Predator abundance strongly related to prey abundance	Can increase <i>or</i> decrease prey extinction risk
Omnivorous	3	Many prey species	“Matrix tolerant” can persist in non prey habitat but with higher mortality rate	Predator abundance partially related to prey abundance	Increase prey extinction risk
Generalist	7	Many prey species	“Matrix based” live primarily in matrix but can also occur in prey habitat	Predator abundance not limited or regulated by prey abundance	Increase prey extinction risk

2 METHODS

2.1 Study species

2.1.1 Bank vole (*Myodes glareolus*)

Bank vole is a common habitat generalist rodent having a wide geographical range in the Palearctic (Macdonald 2001). Bank vole is omnivorous in its diet which includes aerial and underground parts of the plants, seeds, fruits, mosses, lichens, fungi and invertebrates (Butet & Delettre 2011). During the non-breeding season, bank voles are assumed to overwinter in small aggregations in winter nests (Ylönen & Viitala 1985). In Central Finland, bank vole's breeding season starts usually in April and it last until the September. Bank vole females are strictly territorial during the breeding season, since a territory is a necessity for maturation and breeding (Kalela 1957, Bujalska 1973, Ylönen et al. 1988). Female bank vole home ranges are smaller than male home ranges which extend over several female home ranges (Bondrup-Nielsen & Karlsson 1985; Ylönen et al. 1991). Bank voles exhibit post-partum estrus in which female mates within one or two days after parturition (Seabloom 1985, Koskela et al. 1998, Macdonald 2001), allowing the bank vole to produce several litters in a relatively short breeding season. Bank vole has a promiscuous mating system (Klemme et al. 2006) most likely evolved to prevent infanticide by males (Klemme & Ylönen 2010). More than one third of adult male bank voles are infanticidal (Ylönen et al. 1997, Ylönen & Horne 2002). Ylönen et al. (1997) have suggested that infanticide is so common that it might have considerable effects on bank vole populations.

Experimental voles were captured from nature or bred in captivity and housed individually after weaning age (20 days) in standard mouse cages with wood shavings and dry hay as bedding material in the Konnevesi Research Station's animal house. Water and food in the form of rodent pellets (LabFor) were available ad libitum. Light regime in the laboratory was 18L: 6D during summer and 12L: 12D from September onwards.

2.1.2 Least weasel (*Mustela nivalis nivalis*)

The least weasel is a small mustelid specialised on hunting small mammals like voles, mice and shrews. In Finland, weasel populations follow the vole cycles with an approximately half year time lag (Korpimäki et al. 1991) and thus is solely dependent on voles as major food source. Weasels are solitary, except breeding females which are holding a foraging territory during the breeding season (Erlinge 1974, 1975). Weasels, like all mustelids, have a strong distinguishable smell. Prey species can assess predation risk reliably based on scent leaved behind by weasels in the form of feces. Weasels used in the experiments were housed singly in $60 \times 80 \times 60 \text{ cm}^3$ cages with wood shavings and hay bedding in an outdoor shelter at the Konnevesi Research Station.

2.2 Experimental procedures

All the experiments were carried out in the enclosure areas near the Konnevesi Research Station $62^{\circ}41' \text{ N}$, $26^{\circ}17' \text{ E}$. Enclosures are $50 \text{ m} \times 50 \text{ m}$ (= 0.25 ha) in size and made of galvanized steel sheet. The fence reaches 0.5 m under the ground and 0.75 m above ground and prevents voles from escaping and small mammalian predators from entering to the enclosures. Before building the enclosures, the field was ploughed, smoothed and meadow grass seed mixture sown to make the vegetation homogenous and equal between enclosures. Avian predators had free access to the enclosures. We manipulated avian predation risk in the enclosures by mowing the vegetation in enclosures so that the protective tall grass habitat was in the form of one, two or four habitat patches of equal total size of 900 m^2 (Fig. 1, I and IV). In experiments II and III, We used only one and four patches enclosures. In winter experiments IV-V, also enclosures totally covered with tall-grass habitat (2500 m^2) without habitat manipulation were used. In the matrix area surrounding the patches, vegetation was kept totally absent or low (0 - 10 cm) by frequently removing it to the ground level. Subsequent vegetation growth was prevented with the herbicide Round-Up®. The matrix area was considered inhospitable because it did not offer food or safe refuges for voles or weasels.

Space use (I, II, III and IV), survival (I, II, III, IV and V) and condition (I, III, IV and V) of animals were monitored by live-trapping and radio-tracking. Ugglan multiple capture traps (Ugglan special, Grahnbab ab, Hillerstorp, Sweden) were used in the habitat patches and in the matrix in all enclosures (see Fig. 1 for trap configuration). Traps inside the habitat patch were covered with trap chimneys $40 \times 40 \times 50 \text{ cm}^3$ made of metal sheet, and matrix traps by $25 \times 15 \times 2 \text{ cm}^3$ sized wood piece to protect traps from direct sunlight and rain. The protective trap chimneys also allowed trapping during snowy winter. During trapping a mixture of whole oat and sunflower seeds were used as bait. We were measuring the proportion of gravid females (I, IV and V), pups produced per enclosure (IV and V), and pup survival per gravid female (III). In

winter experiments (IV and V), we measured the condition as a weight change from the start of the experiment until the first individuals attained breeding condition and onset of breeding season of the individuals based observations during trapping. In analyzing movements from trapping data or from radio-tracking data we calculated movement areas with Ranges VI (Anatrack ltd. Wareham, UK). Besides movement areas we were measuring the amount of matrix in the movement area of voles and weasels (I, II and III). This measure describes the risk-taking of individuals, ie. how much individuals move outside avian predator safe habitat patch.

The study animals were marked individually with ear tags (Hasco Tag Company, Dayton Kentucky U.S.A, type 1005-1). The age-, weight- and origin- (lab/enclosure-born individuals) distribution was as similar as possible in all experimental enclosures. No relative voles were placed in the same enclosure.

Infanticidal behaviour testing protocol of experimental males is described in more details by Vihervaara et al. (2010). In infanticidal tests one 3 - 5 days old pup was placed into a wire mesh tube and tube was placed into the large rodent cage and male behaviour was observed through one -way mirror. Infanticidal behaviour was classified as follows: Infanticidal; when the vole had bitten and handled roughly the pup tube at least three times. Non-infanticidal; after ten minutes of ignorance, pup was removed from the wire mesh tube. If the male ignored the non-protected pup as well, it was classified as non-infanticidal.

Granivorous-omnivorous bank vole is an excellent study organism compared to more herbivorous vole species because it is easy to manipulate the amount and quality of food for supplemental feeding. Food manipulation in form of sunflower seeds (I and IV) or more nutritious cakes, made of 4.5 g of hera80 protein and 15 g sunflower seeds, were used (V). Ingredients for the cakes were chosen based on earlier studies, so that they included both plant (Ylönen & Eccard 2004) and animal protein (Von Blanckenhagen et al. 2007, Eccard & Ylönen 2001) known to be especially important after long winter for the onset of breeding.

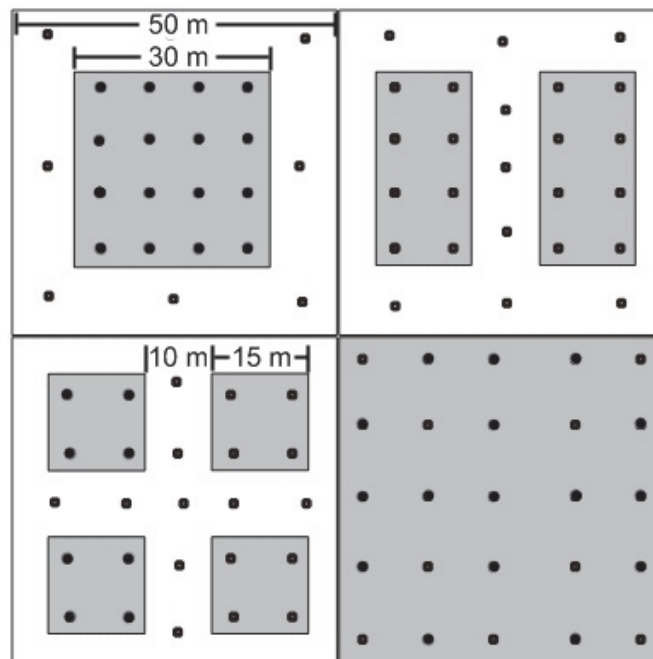


FIGURE 1 Layout of experimental enclosures used in the experiments. Grey represent habitat area, white show matrix area and small black squares represent trap locations. In different studies different combinations of fragmentation types were used. In experiment (I) one patch, two patches and four patches enclosures were used. One patch and four patches enclosures were used in (II and III). All enclosure types were used in (IV) and only enclosures with full habitat cover were used in (V)

3 RESULT AND DISCUSSION

3.1 The effect of habitat fragmentation on individual movements

Habitat fragmentation affects especially the movement of the individuals between suitable habitat patches (Fahrig & Merriam 1994). We were measuring the movements of the bank voles in all fragmentation experiments (I, III and IV). In addition, movements of radio-tracked weasels were recorded in experiment II.

The presence of receptive females activated males to move more (I). This supports previous studies suggesting that females are the key resource for males during the breeding season (Ims 1988, Lin & Batzli 2004). Males had largest movement areas in more fragmented enclosures. Male movement areas without females and at high female density stayed at a similar level regardless of fragmentation treatment. This seemed to be true also in experiment IV where fragmentation increased movements of the voles only in spring when the voles started to attain breeding condition after winter. Longer movements in the more fragmented habitat are reported also in earlier experiments (Diffendorfer et al. 1995, Andreassen et al. 1998). Males also took more risks by moving more in the matrix when trying to improve their mating success in more fragmented habitat (I, Ims 1988). However, infanticidal males (III) moved more regardless of habitat fragmentation treatment probably because high testosterone level which is shown to be related to infanticidal behavior (Ogawa et al. 1998), activity and dominance (Mills et al. 2009). High testosterone level may also increase risk-taking in males. Non-infanticidal males were forced to move out from safe habitat probably due to aggressively nest protecting females (III). Radio-tracking revealed that female vole movement areas were smaller and mean movement distances shorter in the fragmented breeding habitat compared to females in the non-fragmented treatment (III). This indicates that habitat configuration forced females to guard more intensively the nest site (Ylönen & Horne 2002, Liesenjohann et al. 2011) as small patch inhabiting females avoided moving out into the risky matrix habitat similarly like in

Andreassen et al. (1998). In the fragmented enclosures with four patches, weasel movements included more fixes in the risky matrix area, as predicted (II). Thus, despite of high avian predation risk weasels took risks in crossing the open areas. The most plausible explanation is that the small fragments containing 1-2 prey items becomes empty, or the search costs are increasing (Brown 1988) and hunting reward compared to hunting effort decreases. Hunger forces individuals for increased risk-taking in any system with depleting food patches (Brown et al. 1997, Ylönen et al. 2002).

3.2 The effect of food on survival and distribution of individuals in fragmented habitat

Infanticidal males moved more and female voles in small fragments stayed close to their nest indicating more intensive nest guarding. However, there was no significant difference on the number of pups per pregnant female between fragmented and non-fragmented treatments (III). However in total, the small fragment populations produced almost double of recruits, 81, into the 12 populations compared to 48 in the continuous one patch habitat. There was also tendency that there were more gravid females in more fragmented enclosures (I and IV). This might be due to less disturbing social interactions in more fragmented habitat like shown in an experiment by Andreassen et al. (1998) where root vole (*Microtus oeconomus*) home range overlap decreased with fragmentation. Several studies also indicate the higher densities in more fragmented habitats (Chalfoun 2002), for example in the case of the white-footed mice (*Peromyscus leucopus*) (Nupp & Swihart, 1996; 2000). Also, the study of Collins & Barrett, (1997) on meadow voles (*Microtus pennsylvanicus*) showed the higher densities of voles in the fragmented habitat, especially female densities were substantially higher in small patches. The authors suggested that females in fragmented habitats were better able to defend territories leading to better breeding success, while young males were forced to disperse and hence were vulnerable to the avian predation risk in the open matrix habitat. Wolff et al. (1997) suggest that lower rate of infanticide reflected in higher densities in small fragments compared to larger ones.

Females' distribution in one patch enclosures where other half of the enclosure was food supplemented resembles ideal despotic distribution because there were less females in the food side of the habitat patch than in the no food side (I). In enclosures, where there was a matrix between the food patch and no food patch, there was almost one third more females on the food side of the enclosure, resembling ideal free distribution.

I predicted that similarly like voles, weasel stays inside the covered habitat as long as there is prey available, meaning that weasel would kill more voles in the continuous habitat, like suggested in a model simulation by Dalkvist et al. (2011) and Ryall & Fahrig (2006) in their review of theoretical papers. My

results support this hypothesis and I found improved survival of voles in fragmented habitat, but only during autumn when avian predation pressure was high and weasel energy need was increased due to cold weather (II). During this season weasel is known to kill more for hoarding purposes as well, phenomenon called “surplus killing”.

The main result of the experiment IV was that out of the two factors studied, breeding habitat fragmentation and food, the latter was more important on overwintering success of bank voles. Additional food, like shown in many previous studies (for review Boutin 1990) strongly affected condition, trap visiting activity and density of overwintering voles. Fragmentation had an effect on vole movements and risk-taking but only in April due to breeding related behaviors. However, fragmentation did not have any effect on overwintering density.

3.3 Habitat fragmentation and seasonality

3.3.1 Survival

According to my prediction, snow protected the ground-dwelling voles and evened out habitat differences during mid-winter and I did not detect density, or other differences between habitat fragmentation treatments during winter (IV). The survival estimates of the founder individuals of overwintering populations were highest in no predation risk and lowest in the increased predation risk treatments regardless of food supplementation (V). Predation risk, even without direct predation, decreased survival probability to next trapping session ca. 10%. More remarkably, during the most adverse periods in autumn and spring, when the overall survival was lowest, the effect of predator odour was close to 20 %. Mere predation risk has been recognized as an important factor to negatively affect behaviour and consequently also population processes (for review Creel & Christianson 2008). It caused lower densities in predation risk treatment than in other treatments, especially in males, and a generally lowered body condition measured as weight change. The experiment supported ideas proposed by (Preisser et al. 2005) about almost as a strong negative population effect of sole predator intimidation than actual predation. Predation risk (Hik et al. 2001, Sheriff et al. 2009, Trebatická et al. 2010) and food depletion (Kusumoto 2009) can increase stress of an individual. Predation risk induced increased stress levels may have caused negative physiological effects observed in our experiment. Lower fitness of individuals experiencing predator stress may be due to escaping predation risk by movements out of sub-nivean space on the snow and in many cases those males may well be regarded to be “scared to death” (Preisser et al. 2005).

3.3.2 Food

Surprisingly, food supplementation did not increase survival or condition during winter significantly (V). However, voles with supplemental food started to breed first and predator odour treatment delayed the onset of breeding by almost a month compared to food supplementation treatment (V) which was in accordance with other food supplementation studies (Ylönen & Eccard 2004, von Blanckenhagen et al. 2007). Similarly food enhanced onset of breeding also in experiment (IV). However, not all the females even in food supplement treatment were breeding, probably because of density-dependent social breeding suppression for subordinate females (Eccard & Ylönen, 2001). It seems that area of 900 m² of breeding habitat, regardless of fragmentation, was not enough for all surviving females to establish own breeding territory (Bujalska 1985, Ylönen et al. 1990). Without food supplementation the spring density of females was significantly lower and females significantly lighter. Female weight development clearly followed the gradient of food supplementation (IV). Surprisingly, the overall food effect seemed to be stronger in experiment IV compared to V. This might be due to fact that in experiment IV supplemental food contained only lots of sunflower seeds, compared to better quality but lower quantity of sunflower seed-animal protein cakes in experiment V. These observations strongly suggest that both the quality and quantity of food matter. Food had also a strong effect on trappability, in a manner that in no-food enclosures voles' trappability was higher (IV). When supplemental food was provided and voles were in good condition they were not so keen to seek food in the form of bait in the traps. Furthermore, higher densities in food enclosures might have increased negative social interactions decreasing trappability (Viitala & Hoffmeyer, 1985, Ylönen et al. 1990).

4 CONCLUSIONS

In this thesis I have studied how small-scale breeding habitat fragmentation, seasonality and predation affect behaviour and survival of bank voles. The results of my enclosure experiments suggest that habitat fragmentation affects spatial behaviour of both prey, the voles, and their specialist mammalian predator, the least weasel. These effects seemed to be sex and species specific so that male bank voles and predator weasel increase movements, and female bank vole decrease their movements in more fragmented habitat. Matrix area usage and thus risk-taking behaviour by male voles and weasels increased with increasing habitat fragmentation in both cases due to search for more resources. For male voles the most important resource worth to take risk are the receptive females and for weasels the prey, voles. Despite of risk-taking in more fragmented habitat, I did not find any significant differences in survival. In terms of survival, it does not matter if you take risk by leaving safe habitat in continuous or more fragmented landscape. Females in the more fragmented habitat moved less and stayed closer to their nest compared to females in continuous habitat. I was expecting this to reflect in to better pup survival from the teeth of infanticidal males, but I did not found any clear evidence for it. Infanticidal male movements were wider, regardless of the habitat type. Thus there may be strong counter-forces against infanticide, such as aggressive nest protection by the mother. Females in continuous habitat produced less pups than females in fragmented habitat, probably due to more interactions with conspecifics competitors. I have also studied predator-prey relationships in fragmented landscape, when the predator is a specialist, dependent on one prey type. I found that for the specialist predator's point of view it is better to live in continuous habitat where hunting is more successful in the short term, but for the persistence of the both prey and predator fragmented habitat where prey can escape predators more easily, might be more sustainable. These experiments indicate that habitat fragmentation might be even beneficial to the small rodent populations. Especially less mobile females might benefit from fragmentation which causes less intra and/or interspecific distraction around nest site. This might lead to higher survival and improved reproduction result.

Habitat fragmentation seems to have only minor importance for voles during winter with a permanent snow cover. When the snow melts and voles entered breeding condition and start to compete for optimal territories, habitat fragmentation became again as important as during the breeding season. Predator odour had strong effects on survival probabilities, density and condition of overwintering voles. At the onset of breeding, the food was more important compared to predation risk. That could mean that as an individual has 'decided' to breed despite the possible increased risk of predation, it uses all means to gain more energy for successful reproduction. Both food quantity and quality seem to be important for fitness of an individual over winter. Small amount of high quality food may enhance onset of breeding but large quantity is important for better condition and weight gain. My experiment clearly verified an effect of increased predation risk delaying breeding after non-breeding season. Thus, environmental constraints like harsh winter may be the kind of restrictive condition in addition to risk of predation which affects individual breeding strategies.

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YHTEENVETO (RÉSUMÉ IN FINNISH)

Ympäristön pirstoutumisen, vuodenaikaisvaihtelun sekä petojen vaikutus metsämyyrän käyttäytymiseen ja hengissä selviytymiseen

Maapallolla on meneillään kuudes sukupuuttoaalto, jonka seurauksena noin puolet maailman kasvi- ja eläinlajeista on vaarassa kadota. Suurin syy lajien eli biodiversiteetin vähenemiseen on elinympäristöjen häviäminen ja pirstoutuminen pieniin eristyneisiin laikkuihin ihmisen toiminnan, kuten metsien raivaamisen viljelyskäyttöön, seurauksena. Syy siihen, ettei sukupuuttoaalto ole vielä näyttäytynyt koko voimallaan on sukupuuttovelka eli aikaviive elinympäristön tuhoutumisen ja lajin häviämisen välillä. Ilmastonmuutoksen odotetaan edelleen voimistavan sukupuuttoaaltoa. Näin siksi, että ilmaston lämpenemisen ja tästä aiheutuvien elinympäristömuutosten vuoksi lajien on joko mukaututtava uusiin elinoloihin tai kyettävä liikkumaan uusille soveliaille elinalueille. Pirstoutuneessa elinympäristössä yksilöiden liikkuminen sopiviin elinympäristölaikkuihin ja sopivien elinympäristöjen löytyminen on kuitenkin vaikeampaa. Lajien sukupuuttoriskiä lisää entisestään se, että eläinten käyttäytyminen ja sosiaalinen kanssakäyminen voivat pirstoutuneessa elinympäristössä muuttua.

Selvitin väitöskirjassani ympäristön pirstoutumisen, vuodenaikaisvaihtelun ja petojen vaikutusta eläinten käyttäytymiseen ja tilan käyttöön sarjalla tutkimuksia, jotka tehtiin kokeellisesti pirstoutuissa elinympäristöissä. Tarkoitukseni oli löytää mekanismeja, jotka aiheuttavat useissa tutkimuksissa ympäri maailmaa havaittuja eläinpopulaatioiden pienenemisiä. Tutkimuslajeina käytin Suomen yhtä yleisintä nisäkäslajia metsämyyrää (*Myodes glareolus*) sekä pikkunisäkkäiden saalistamiseen erikoistunutta lumikkoa (*Mustela nivalis nivalis*). Myyriä on myös aiemmin käytetty menestyksellisesti ympäristön pirstoutumista käsittelevissä tutkimuksissa, ja tutkimustuloksia on pystytty myös soveltamaan muun muassa vaikeammin tutkittavissa olevien lajien tilankäyttöön pirstoutuneissa metsissä.

Koeympäristönä toimi pitkää heinikkoa kasvava vanha pelto, jonne oli rakennettu yhteensä 20 kpl 50 x 50 metrin suuruista myyränpitävää aitausta. Koeaitausten heinikkoon leikattiin ympäristön pirstoutumista jäljitteleviä kuvioidia. Näiden kuvioiden välinen alue oli avointa myyrille suojatonta maastoa, joka ei tarjonnut myöskään ravintoa. Petolintujen saalistusta ei ollut alueella estetty. Myyrien ja lumikoiden liikkeitä aitauksissa seurattiin elävänä pyytävillä loukuilla sekä radiotelemetrian avulla. Manipuloin kokeissa ympäristön pirstoutumisen lisäksi resursseja eli ravintoa ja naaraiden lukumääriä, saalistuspainetta sekä poikasia tappavien urosten läsnäoloa.

Väitöskirjani koostuu viidestä osatutkimuksesta, joista kolme tein kesällä ja kaksi talvella. Kesällä tehdyissä kolmessa kokeessa sekä ensimmäisessä talvikokeessa tutkin ympäristön pirstoutumisen vaikutuksia metsämyyrän ja lumikoiden käyttäytymiseen. Toisessa talvikokeessa tutkin saalistusriskin ja

ravinnon vaikutuksia metsämyyrän talven yli selviytymiseen, niiden kuntoon ja lisääntymisen aloitukseen.

Tutkimustulokset osoittivat, että ympäristön pirstoutuminen kasvattaa metsämyyräkoiraiden liikkuma-aloja. Lisäksi metsämyyräkoiraiden ja lumikoiden riskinotto eli liikkuminen kuvioiden välisellä alueella edelleen lisääntyi, jos resurssit eli kiimassa olevat naarat metsämyyräkoiraille ja ravinto eli myyrät lumikoille, olivat jakautuneet tasaisesti eri pirstoutuneille elinympäristölaikuille sen sijaan, että resurssit olisivat jakautuneet tasaisesti yhtenäisessä elinympäristössä. Metsämyyrät ja niitä vain hieman suuremmat lumikot ovat kuvioiden välisellä alueella suuressa vaarassa jäädä petolintujen saaliiksi.

Myyrien selviytymisessä koetarhoissa ei kuitenkaan havaittu eroja pirstoutuneen ja yhtenäisen elinympäristön välillä, ja avoimella alueella liikkuminen näyttikin olevan myyrille yhtä vaarallista riippumatta siitä, eläkö se yhtenäisessä vai pirstoutuneessa elinympäristössä. Tutkimus osoitti, että poiketen koiraista metsämyyränaaraat pysyttelivät pääosin elinympäristölaikkunsa sisällä niin yhtenäisissä kuin pirstoutuneissakin elinympäristöissä sekä sen, että naaraat liikkuvat pirstoutuneissa elinympäristöissä pienemmällä alueella kuin yhtenäisessä elinympäristössä. Naaraat pysyttelivät pirstoutuneissa elinympäristöissä myös lähempänä pesäänsä, jolloin niillä on parempi mahdollisuus suojella poikasiaan mahdollisilta pesän ryöstäjiltä kuten vieraita poikasia tappavilta koirasmyyriltä. Pirstoutunut elinympäristö näyttikin tulosten perusteella tuottavan hieman enemmän poikasia kuin yhtenäinen elinympäristö. Syynä tähän on pesän lähellä pysyttelemisen lisäksi luultavasti se, että pirstoutuneessa ympäristössä naaras pystyy valtaamaan reviiiriseen koko laikon, jolloin sen elinympäristössä on vähemmän muiden myyrien aiheuttamaa häirintää ja puolustautumistarvetta. Tutkimustulokset eivät poikastuotannon eroista huolimatta kuitenkaan osoittaneet eroja poikasten selviytymisessä pirstoutuneen ja yhtenäisen elinympäristön välillä, kun tarkasteltiin naaraskohtaista poikastuottoa.

Poikasten selviytymiseen ei vaikuttanut myöskään se, oliko tarhoissa oletettavasti korkean testosteronitason omaavia metsämyyräkoiraita, jotka tappavat vieraita poikasia, vai ei poikasia tappavia koiraita. Eroa ei havaittu siitäkään huolimatta, että poikasia tappavat koiraat liikkuvat suuremmalla alueella kuin ei poikasia tappavat koiraat riippumatta ympäristön pirstoutuneisuudesta.

Tutkimustulokset eivät osoittaneet eroja lumikoiden liikkuma-aloissa yhtenäisen ja pirstoutuneen elinympäristön välillä. Lumikoiden havaittiin kuitenkin saalistavan tehokkaammin yhtenäisissä elinympäristölaikuissa, mutta vain syksyllä. Tämä johtunee siitä, että syksyllä petolintuja on enemmän, jolloin saalistaminen yhtenäisessä laikussa on lumikolle saalistuspaineen vuoksi tehokkaampaa sekä siitä, että viileämmästä säästä johtuen myös lumikoiden ravinnon tarve on syksyisin suurempi. Lisäksi lumikot saattavat säiden kylmetessä saalistaa varastoon, jolloin erot yhtenäisen ja pirstoutuneen elinympäristön välillä suuren petopaineen alla korostuvat.

Ensimmäisen talvikokeen tulosten perusteella havaitsin, että metsämyyrien käyttäytymisen osalta suojaava lumikerros tasoittaa erot pirstoutuneen- ja yhtenäisen elinympäristön välillä. Kuitenkin keväällä lumen sulaessa ja myyrien lisääntymiskauden alkaessa pirstoutuneessa ympäristössä elävät koiraat ovat pakotettuja yhtenäisessä elinympäristössä eläviä koiraita suurempaan riskinottoon, mikäli ne aikovat paritella kiimassa olevien naaraiden kanssa. Talviaikaisella lisäravinnolla havaittiin olevan positiivisia vaikutuksia myyrien kuntoon, jota mitattiin yksilöiden painonkehityksellä alkutalvesta lisääntymiskauden alkuun. Lisäravinto vaikutti positiivisesti myös myyrien talven yli selviytymiseen sekä lisääntymisen aloitusajankohdan aikaistumiseen. Viimeinen talvikoe osoitti, että talviaikana jo pelkällä saaliiksi jäämisen riskillä, eli pelkän lumikon hajun levittämällä tarhoihin ilman varsinaista pedon läsnäoloa, oli dramaattisia vaikutuksia myyriin: lumikon haju heikensi myyrien kuntoa ja vähensi erityisesti koiraiden selviytymistä talven yli. Saaliiksi jäämisen riski johti pienempiin populaatiokokoihin sekä lisääntymisen aloituksen myöhästymiseen jopa kuukaudella. Saalistuksen epäsuorat vaikutukset saaliin selviämiseen ja elinkykyyn ovatkin vastoin yleistä käsitystä paljon pelkkää saaliin tappamista laajemmat.

Tutkimukseni osoittavat, että ympäristön pirstoutuminen aiheuttaa muutoksia sekä yksilöiden käyttäytymiseen että yksilöiden väliseen sosiaaliseen kanssakäymiseen, josta seuraa edelleen muutoksia sekä yksilöiden että kokonaisten populaatioiden elinkykyyn. Ympäristön pirstoutumisen aiheuttamat muutokset eläinten käyttäytymisessä ja elinkyvyssä ovat kuitenkin monimutkaisia syy-seuraussuhteita, mistä syystä ympäristön pirstoutumisen vaikutuksia eläinten käyttäytymiseen ja elinkykyyn sekä vaikutuksen suuntaa on vaikea ennustaa. Lisäksi havaitut muutokset yksilöiden ja populaatioiden elinkyvyssä riippuvat aina myös kokeiden mittakaavasta ja niiden kestosta.

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ORIGINAL PAPERS

I

EFFECT OF FRAGMENTED BREEDING HABITAT AND RESOURCE DISTRIBUTION ON BEHAVIOUR AND SURVIVAL OF THE BANK VOLE (*MYODES GLAREOLUS*)

by

Marko Haapakoski & Hannu Ylönen 2010

Population Ecology 52: 427-435

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II

MAMMALIAN PREDATOR-PREY INTERACTION IN A FRAGMENTED LANDSCAPE: WEASELS AND VOLES

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III

INFANTICIDE EFFECTS ON BEHAVIOR OF THE BANK VOLE (*MYODES GLAREOLUS*) IN THE FRAGMENTED HABITAT

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IV

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Marko Haapakoski & Hannu Ylönen 2012

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V

**PREDATION RISK AND FOOD: OPPOSITE EFFECTS ON
OVERWINTERING SURVIVAL AND ONSET OF BREEDING IN
A BOREAL RODENT**

by

Marko Haapakoski, Janne Sundell & Hannu Ylönen 2012

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