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POPULATION DYNAMICS AND BEHAVIOUR IN TWO *MICROTUS* VOLES: EFFECTS OF INTERSPECIFIC COMPETITION AND MULTIPLE PREDATORS

by

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III Koivisto, E., Huitu, O, Hoset, K. S. and Korpimäki, E. Density-dependent habitat distribution of coexisting vole species under predation risk. – *Submitted manuscript.*

IV Koivisto, E. and Pusenius, J. 2003. Effects of temporal variation in the risk of predation by least weasel (*Mustela nivalis*) on feeding behavior of field vole (*Microtus agrestis*). – *Evolutionary Ecology* **17:** 477-489.

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1. Introduction

Species are seldom, if ever, alone in nature. On the contrary, natural communities are usually complex assemblages consisting of a number of interacting species. Coexistence requires species to differ in some way: if there are two very similar species in the community, one of them will replace the other (the theory of limiting similarity of species, MacArthur and Levins 1967). A niche defines a species' place in an ecosystem, like a piece of a puzzle, and also the functional relationships of the species to other organisms as well as abiotic factors. A niche can be seen as a function of four different factors: resources, natural enemies, space and time (Amarasekare 2003). Competing with other species is costly, reducing time and energy from other necessary activities, like foraging and mating. Therefore, species evolve to avoid interspecific competition by niche separation. Species can use different resources (MacArthur and Levins 1967) or vary in their susceptibility to predation (Murdoch and Oaten 1975). Temporal niche partitioning occurs when species use the same resources at different times (Armstrong and McGehee 1976), for example when one species is nocturnal and the other diurnal. Species may also differ in where they use the resources (spatial niche partitioning, May and Hassel 1981, Chesson 2000). Of course, all coexisting species do not compete, and neither is niche separation necessarily caused by competition.

1.1 Competition

Competition refers to an interaction that is harmful to both parties and which can occur between individuals of the same species (intraspecific competition) or between different species (interspecific competition). It can be further divided into interference competition and exploitative competition. Interference competition means direct, often physical interactions, such as fighting over territories. Species can also compete with each other indirectly via exploitation, i.e. using resources so they become no longer available to others (e.g. Schoener 1983).

In extreme cases, interspecific competition for limiting resources can make the co-occurrence of two species impossible, leading thus to the local extinction of one species (the competitive exclusion principle, Gause 1934, Koplin and Hoffmann 1968, Morris and Grant 1972). Even when local coexistence is possible, interspecific competition may still have strong negative effects on both competing species. Interspecific competition has been studied widely in many animal groups including small mammals, and particularly rodents (for reviews see Grant 1972, Eccard and Ylönen

2003). In voles there are several examples where interspecific competition has been shown to have negative effects on population growth, survival or reproductive success of species. For example, in the absence of potential competitors, bank voles (*Myodes glareolus*) reached densities twice as high as during sympatry (Löfgren 1995). The survival of female bank voles was reduced under competition with field voles, *Microtus agrestis* (Eccard and Ylönen 2002). On the other hand, there are also a number of cases where the presence of another closely related species seemed to have only minor or no obvious effects (e.g. Lin and Batzli 2001, Johannesen 2003).

1.1.1 Habitat selection

There are number of studies on small mammals in various ecosystems concerning the effects of interspecific competition on habitat selection or space use. For example, Egyptian sand gerbils (*Gerbillus pyramidum*) forced Allenby's gerbils (*G. andersoni allenbyi*) to forage in a less preferred habitat type through interference competition (Ziv et al. 1993). Bank voles reduced their space use in the presence of field voles (Eccard and Ylönen 2002). An experimental reduction of meadow voles (*Microtus pennsylvanicus*) induced movements of montane voles (*Microtus montanus*) into the vacated habitat (Koplin and Hoffmann 1968). The wood mouse (*Apodemus sylvaticus*) changed its nesting place preferences from above to down on the ground in the presence of yellow-necked mice, *A. flavicollis* (Hoffmeyer 1973).

The outcome of competitive interactions can vary according to habitat. For example, meadow voles used woodland less in the presence of Southern red-backed voles (*Myodes gapperi*), even though the meadow vole is the dominant species in grassland (Morris and Grant 1972). Also density is known to affect habitat selection; Allenby's gerbils were about twice as likely to be caught in the favoured habitat and spent more than twice as much time there at low densities and in the absence of Egyptian sand gerbils (Abramsky et al. 1990).

In many of these studies, however, effects of predation have not been controlled for, even though predation can alter interspecific competitive interactions substantially (for reviews see Sih et al. 1985, Gurevitch et al. 2000, Chase et al. 2002). In fact, predation may even override the effects of interspecific competition altogether (Abramsky et al. 1998, see also Lin and Batzli 2001). A model by Grand and Dill (1999) examines how two types of competitors distribute between productive, but risky, habitat and poor, but safe, habitat in a situation where the competitors differ both in their competitive abilities and susceptibility to predation. The model predicts that when species experience different ratios of mortality risk across the habitats and mortality risk is diluted by numbers, both species tend to aggregate in a single habitat. When superior competitors experience a higher ratio of mortality risk between habitats than inferior ones do, both species aggregate in the risky, but productive, habitat. Similarly, when inferior competitors are the ones experiencing higher risk ratio, both species tend to aggregate in the safer, but less productive, habitat (Grand and Dill 1999).

1.2 Predation

For an individual prey an encounter with a predator usually means getting either killed or injured. For a population, however, effects can be varied. In the worst case, from the point of view of the prey, the predator can cause a local extirpation or even a global extinction of the prey species (e.g. Fritts and Rodda 1998). Unselective predation decreases the population density of prey, which can decrease chances of finding a mate or reduce the genetic variation of the population (e.g. Frankham 1996). Selective predation on certain pheno- or genotypes (e.g. Galeotti et al. 2005) or a particular size or age group (e.g. Sogard 1997) or sex (e.g. Norrdahl and Korpimäki 1998), can alter the population structure, and therefore the viability or reproductive success, of the prey population (e.g. Banks et al. 2000).

Predators can also affect their prey indirectly, by their mere presence. Prey can detect the presence of a predator from a variety of signs, visual, auditory or olfactory, and use them as cues to estimate current risk level and respond accordingly. Preisser et al. (2005) suggest that resulting indirect, or non-lethal, responses to predators can be as strong as those of direct consumption. Such indirect effects of predation (also called intimidation) have been widely studied, especially among rodents. There are several studies showing responses of small mammals to olfactory or auditory cues of predators (see Norrdahl and Korpimäki 2000, Ylönen and Brown 2007 for reviews). These responses (antipredatory behaviour) may include, for example, decreased feeding activity, reduction of movements (Norrdahl and Korpimäki 1998) or moving to a safer habitat, all of which may in turn affect rates of survival and reproduction. The overall effect that a predator has on a prey community is thus commonly more than just the direct consumption of individuals. Also the effects of predation do not necessarily cease when the predator leaves the area but can continue to affect prey even after that, e.g., through time delays associated with a temporary cessation of reproduction due to predation risk (e.g. Sih 1992).

1.2.1 Risk allocation

Actively hunting predators are usually very mobile. Thus, the risk of predation perceived by their prey tends to vary in time. Due to the trade-off between antipredatory behaviour and other fundamental activities, such as feeding and mating, prey should greatly benefit from an ability to adjust their level of vigilance to the variation in the current level of risk. It seems that many animals possess this ability (Kats and Dill 1998). The "predation risk allocation hypothesis" by Lima and Bednekoff (1999) explains how temporal variation in risk affects allocation of antipredatory behaviour and foraging effort across different risks of predation. The hypothesis states that an animal's response to predation risk at one time period should depend on the risk experienced at other times. In an environment with a variable risk of predation, the animal spends a certain part of its time in a high risk situation (p), and the rest of it ($1 - p$) in a less dangerous situation. In a high risk situation the attacks of the predator occur at rate α_H and in a low risk situation at rate α_L. The animal has to decide how much foraging effort (or vigilance) to allocate across the two risk states such that survival is maximized and that energy requirements are met.

According to Lima and Bednekoff (1999) the attack ratio (α_H/α_L) and the time spent in a high risk situation (p) are the main factors affecting allocation decisions. When attack ratio increases ($\alpha_H > \alpha_L$) a prey animal decreases its foraging effort in high risk situations and increases it in low risk situations. The increase of p, on the other hand, may force the animal to forage also during high risk situations to meet its energy requirements. Of course, in these conditions the animal tries to forage as efficiently as possible also during the short periods of lower risk between long periods of high risk. Thus foraging effort in both high and low risk situations should increase with an increase of p, but the increase should be even more rapid in low risk situations than in high risk situations, especially when attack ratio is high. On the other hand, the hypothesis predicts the animal to be most vigilant, and feed the least, during short periods of high risk when attack ratio is high.

1.2.2 Multiple predators

Most often prey animals have to avoid not only one, but multiple, predators. Since predators have different hunting techniques, the responses exhibited by prey also vary. Under threat by several types of predators, attempts to avoid one can make prey more vulnerable to another (Kotler et al. 1992, Lima 1992, Korpimäki et al. 1996). For example, diurnal avian predators hunt mostly by vision and, therefore, prefer hunting in open landscapes. Least weasels (*Mustela nivalis*), on the other hand, rely mostly on their senses of smell and hearing. They hunt in cover and are themselves vulnerable to attacks by birds of prey (Korpimäki and Norrdahl 1989, Brandt and Lambin 2007). A vole escaping avian predation from the open to cover can run into the mouth of a weasel, and when escaping from a weasel, it can run into the talons of a bird of prey (Korpimäki et al. 1996).

Predator facilitation results if prey regard one predator more dangerous than the other (Charnov et al. 1976). Voles might regard avian predators as a bigger threat than mammalian ones (Korpimäki et al. 1996), which could increase their exposure to weasels. In an aviary experiment field voles preferred cover in a predator-free situation or when under avian predation alone, but they shifted to open habitat when a least weasel was introduced to the cover (Korpimäki et al. 1996). However, when predation pressure came simultaneously from two types of predators, the least weasel and the Eurasian kestrel (*Falco tinnunculus*), voles behaved as if under risk from kestrel alone. This suggests that voles either perceive the risk by an avian predator as greater than that of a weasel or that a habitat shift as a behavioural response is more effective against raptors than mustelids. Gerbils (*Gerbillus*) responded to the threat of snakes in an opposite manner and increased their exposure to owls (Kotler et al. 1992).

Small-sized predators may also suffer predation from larger-sized predators that exploit the same type of prey (intraguild predation, Polis et al. 1989). In North Europe, there is a diverse assemblage of native vertebrate predators subsisting on small mammals as their main prey. In western Finland, this assemblage includes four different-sized mammalian predators, the red fox (*Vulpes vulpes*), the pine marten (*Martes martes*), the stoat (*Mustela erminea*) and the least weasel, as well as nine avian predators, the eagle owl (*Bubo bubo*), the Ural owl (*Strix uralensis*), the common buzzard (*Buteo buteo*), the hen harrier (*Circus cyaneus*), the short-eared owl (*Asio flammeus*), the long-eared owl (*A. otus*), the Eurasian kestrel, Tengmalm's owl (*Aegolius funereus*), and the pygmy owl (*Glaucidium passerinum*). It is well known that, for example, red foxes kill smaller mammalian predators, in particular small mustelids (Dell'Arte et al. 2007), eagle owls prey on all the smaller avian and mammalian predators (Korpimäki and Norrdahl 1989, Sergio and Hiraldo 2008) and that all the above-mentioned avian predators kill and eat least weasels (Korpimäki and Norrdahl 1989), the smallest member of the vole-eating predator guild.

Intraguild predation can lead to risk reduction for their shared prey, so that the density of the common prey species is positively affected as a result of fewer small predators (Eklöv and Werner 2000, Sih et al.1998, Vance-Chalcraft et al. 2007). Multiple predator species may also cause risk enhancement in prey, however, if the presence of one predator increases the hunting success of the other (reviewed in Sih et al. 1998, Vance-Chalcraft et al. 2007).

Intraguild predation is a widespread phenomenon (Arim and Marquet 2004). Among vertebrate predators, intraguild predation is predictably imposed by larger species on their smaller competitors (Korpimäki and Norrdahl 1989, Palomares and Caro 1999, Sergio and Hiraldo 2008). The predation risk by larger predators is also known to induce behavioural shifts in smaller predators; for example American mink (*Mustela vison*) reduced their swimming distances in response to predation risk by white-tailed sea eagles, *Haliaeetus albicilla* (Salo et al. 2008). Moreover, since removal of mink has been found to increase vole numbers, leading to higher diversity of plants (Fey 2008), intraguild predation may also have effects on trophic cascades (Finke and Denno 2006).

1.2.3 Effects of predation on competition

Predation can alter interspecific competitive interactions substantially (for reviews see Sih et al. 1985, Gurevitch et al. 2000, Chase et al. 2002). For example, coexisting species may have indirect negative effects on each other via shared predators (i.e. apparent competition, Holt 1977), or predators can prefer one prey species over another and thus shape the composition of the prey community by selective hunting (e.g., Slobodkin 1964, Paine 1966, Leibold 1996). Predators may also promote the coexistence of species in a situation where it would otherwise be impossible (Slatkin 1974, Vance 1974, Roughgarden and Feldman 1975, Crowley 1979, Chase et al. 2002, Kondoh 2003). One mechanism is predator switching in which predators disproportionately hunt the most abundant prey species and switch preference as the relative densities of the prey change (Murdoch and Oaten 1975, Roughgarden and Feldman 1975, see also Sundell et al. 2003). Coexistence can also be facilitated by predation if a trade-off exists between the competitive abilities (i.e., efficiency of resource exploitation) and predation resistance of the prey species (Vance 1974, Lubchenco 1978, Leibold 1996). Efficiency in resource exploitation by a superior competitor often translates into high reproductive rates, which on a population level may lead to a clustered spatial distribution of the prey (Kondoh 2003). This, in turn, may predispose the superior competitor to greater predation (e.g. Connell 2000) and ultimately have positive effects on a competing species with lower reproductive rates and a more even spatial distribution (Kondoh 2003). When predation pressure is high, the importance of direct competition can become reduced, only to become more important when predation is low. Therefore, studies on interspecific competition carried out under high predation pressure may give results which underestimate the degree of potential direct competition.

1.3 Aims of the thesis

The main purpose of this thesis was to study biological factors potentially enabling the coexistence of ecologically similar species, using two small mammals, the field vole and the sibling vole (*Microtus levis,* ex *M. rossiaemeridionalis*) as model organisms. To do so, I examined the effects of interspecific competition and predation on population dynamics and behaviour of these coexisting small mammals.

The field vole and the sibling vole are sympatric close relatives which compete for similar resources (Myllymäki 1977a). Previous non-experimental studies have indicated that on a population level the smaller sibling vole is a superior competitor (Norrdahl and Korpimäki 1993), yet more vulnerable to predation than the slightly larger field vole (Korpimäki 1992, Koivunen et al. 1996). Field voles are more numerous in our study area (Huitu et al. 2004), which suggests that predation has a profound influence on the interspecific dynamics of these species in natural surroundings (Norrdahl and Korpimäki 1993). Patch-searching avian predators seem to prefer sibling voles over field voles as prey because of their tendency to live in higher densities (Korpimäki 1992), but the preference of small mustelid predators (least weasels and stoats) is more poorly known. Responses of voles to these two kinds of predators were expected to differ, since mustelid predators tend to hunt in cover, probably because of predation risk by avian predators, while avian predators prefer to hunt in open areas.

In particular, I studied the effects of interspecific competition on population growth of field and sibling voles in chapter I. Based on the previous knowledge, I predicted that in the absence of predators, sibling voles would perform better than field voles under coexistence of the two species

(I). In chapter II I tested the effects of predation on the two species by exposing vole populations to freely-hunting least weasels. Since the high-density spatial aggregations of sibling voles are potentially attractive to predators, I predicted that predation would have a more pronounced effect on population densities of the sibling vole than those of the field vole. If so, predation could potentially contribute to promoting the coexistence of the vole species. Chapter III aims to experimentally evaluate the effects of predation on interspecific competition for habitat types between the vole species and to test the predictions of a model by Grand and Dill (1999). Since sibling voles reportedly prefer shorter grass in nature more than field voles, I predicted that sibling voles would 1) use more short grass than field voles in the absence of predation, but 2) respond more strongly to predation risk by shifting to cover than would field voles. To meet the predictions of Grand and Dill (1999) the two species should aggregate in a single habitat under interspecific competition and predation risk if mortality risk is diluted following increasing population densities. Chapter IV examines the predictions of a risk allocation model of Lima and Bednekoff (1999) by measuring feeding effort of field voles exposed to varying presence of the least weasel or its faeces in laboratory conditions. I asked, 1) if there is a difference in feeding effort between low and high risk situation and if it increases with increasing attack ratio, and 2) does the difference in feeding effort between low and high risk situation increase with increasing proportion of time at high risk? In chapter V I studied whether the presence of the Tengmalm's owl affects the hunting efficiency of the least weasel, as measured by population responses of coexisting prey species. I predicted that if the larger predator reduces the efficiency of the smaller predator and thus induces risk reduction in their shared prey, vole densities are higher following the multiple predator treatment than following the single predator treatment.

2. Material and methods

2.1 Study species

2.1.1 Voles

The sibling vole was probably unintentionally introduced from the Karelian isthmus, north-western Russia, to western Finland in the 1940s (Sulkava and Sulkava 1967), and it now inhabits the agricultural areas near the western coast of the country. The field vole, a close relative of the former, also occurs naturally in the same area. Both species are folivorous and use similar, but not identical, habitats and food resources (Myllymäki 1977a). For example, sibling voles purportedly use shorter grass and cultivated fields more than field voles (Myllymäki 1977a, Norrdahl and Korpimäki 1993). In our study area, the two species show synchronous, high-amplitude, cyclic population fluctuations with a period of three years (Huitu et al. 2004, Korpimäki et al. 2005a). Sibling voles, particularly females, are slightly smaller than the field voles. The body mass (mean ± S.D) of an adult female sibling vole in the study area is 24.6 ± 6.1 g (n=163) and that of an adult female field vole 30.8 ± 7.6 g (n=87) (Norrdahl and Korpimäki 1993), whereas the body mass of an adult male sibling vole is 31.2 ± 6.1 (n=142) g and that of an adult male field vole 32.4 ± 6.7 g (n=137) (Norrdahl and Korpimäki 1993).

2.1.2 Least weasel

Weasels are small, efficient predators that are highly dependent on voles of the genus *Microtu*s for their food source in western Finland and elsewhere in northern Europe (Korpimäki and Norrdahl 1991, Korpimäki et al. 1991, Valkama et al. 2005). In the study area the proportion of voles in the diet of least weasels has never been reported to be < 45% and is usually > 80% (Korpimäki et al. 1991). Least weasels have a long, slender body, which enables them to follow voles into their underground and subnivean burrows. In a study where the fates of radio-collared voles were followed, least weasel predation was found to be the most important cause of death (Norrdahl and Korpimäki 1995). Mammalian predators appear to remove more female than male voles from the population, either because females are easier to find in their nests or because gravid females are easier to catch than more agile and aggressive males (Norrdahl and Korpimäki 1998).

Least weasels and many other members of the mustelid family have a large pair of anal glands containing species-specific substances used for scent marking (King 1989), and voles probably have an innate ability to react to the odours of weasels and other mustelids (Parsons and Bondrup-Nielsen 1996, Bolbroe et al. 2000, Fey 2008).

2.1.3 Tengmalm's owl

Tengmalm's owl is a small, nocturnal predator that usually hunts using a sit-and-wait hunting technique on low perches (Norberg 1970, Bye et al. 1992), primarily at forests edges near open ground (Korpimäki 1988b; Norberg 1970). Its main prey are voles in the genus *Microtus* (e.g. Korpimäki 1988a; Koivunen et al. 1996). Because these owls are opportunistic foragers, the amount of *Microtus* spp. in their diet varies yearly according to prevailing vole abundance (Korpimäki 1988a). Avian predators catch more male than female voles, apparently due to the higher mobility of the former. Avian predators also prefer small prey individuals to large ones (Koivunen et al. 1996).

2.2 Study system

The field experiments (chapters I, II, III, V) were conducted at four study sites during summers and autumns 2004-2007 in Lapua, western Finland (63° N, 23° E). The sites established on old farmland in 1996, are located within 12 km^2, 1.5 -7 km apart from one another. Graminoids, such as canary grass (*Phalaris arundinacea*), and herbs, such as nettle (*Urtica dioica*), creeping thistle (*Cirsium arvense*) and fireweed (*Epilobium angustifolium*) dominate the vegetation. A more detailed description of the vegetation is given in Norrdahl et al. (2002).

At each site there was an enclosure consisting of two separate 0.5-hectare, predator-proof sections, constructed using hardware cloth (mesh size 12.7 mm) extending 0.5 m below and 1.3 m above ground. On the outside, a metal sheet was fastened to the upper 40 cm of the fence to prevent climbing by voles and mammalian predators. On the inside, a sheet of plastic was attached to the upper edge of the fence to ensure that weasels could not leave the enclosure by climbing. To prevent access by avian predators, the enclosures were covered with 10-cm nylon net [mesh size 4 cm in two enclosures in 2007 to keep owls in (chapter V)]. All four sites also contained one 0.5-hectare control area (hereafter control) surrounded by a low fence, which allowed all predators to enter and exit at wish but prevented the dispersal of voles. The low fences of the control areas were ca. 40 cm above ground and extended ca. 60 cm below ground. Each control area had six evenly distributed access points where the top of the fence was lowered to a ca. 30 cm to promote the entry of small mustelids (least weasels and stoats).

Forty-eight multiple capture Ugglan live-traps (Grahnab, Sweden) were distributed evenly ca. 10 m apart in each experimental and control area. The traps were placed individually in plastic boxes (40 x 30 x 25 cm) to provide protection from the weather. The grass of the central third of each enclosure and control was kept short (10 - 20 cm) by mowing. In the unmowed sections, the natural vegetation reached a height of ca. 100 - 200 cm during the experiments. Between the short and the tall grass sections was a ca. 1.5-m wide zone which was treated with herbicide (RoundUp, Monsanto Europe S.A., Belgium) to remove edge vegetation to reduce movements of individuals between habitats. The traps were placed so that one third (16) of them were in the short grass area and two thirds (32) were in the tall grass area.

2.3 Experimental design

2.3.1 Competition

To determine the effects of interspecific competition on the population growth, reproductive parameters (chapter I) and habitat selection (chapter III), four pairs of field voles or four pairs of sibling voles were released in early July 2004 into randomly selected predator-proof enclosures [treatment: “no competition, no predation” (C–P–); n=2 for each species] and two pairs of both species into remaining enclosures [“competition, no predation”, (C+P–); n=4] (chapters I and III) and into the fenced controls [“competition, predation”, (C+P+); n=3] (chapter III). Thus, all replicates were founded with an equal density of voles (8 per pen and 16 per ha). The voles were originally caught in Lapua and surroundings and kept in single-species populations for a month in 0.5-ha predator-proof enclosures. Individuals were allocated randomly to different treatments and areas for the experiment. Only sexually mature individuals were used, as judged by a perforate vagina in females or scrotal testes in males. Vole population growth was monitored by live-trapping on seven occasions from the end of July to the beginning of November, using standard capture-mark-recapture techniques as described below. As an index of habitat selection by an individual vole, the proportion of captures within the short grass section was recorded (chapter III).

2.3.2 Weasel predation

In mid-May 2005 two pairs of field voles and two pairs of sibling voles were released into each of the eight enclosure sections to study the effects of least weasel predation on population growth and reproductive parameters of the two vole species (chapter II). Changes in vole population densities were monitored by live-trapping on six occasions from the end of May to the end of October. Two trappings were conducted before the treatment period to ensure that vole populations had increased sufficiently to support the weasels. The third trapping was conducted just before the release of weasels (see below), the fourth immediately after the removal of weasels and the last two after the treatment period to follow possible delayed effects occurring after the removal of predators. In mid-July we released one radio-collared weasel into each of three randomly chosen enclosure sections. The weasels were allowed to move and hunt freely in the enclosures for three weeks, which corresponds roughly to the time of one vole reproductive cycle (interval between successive parturitions, Innes and Millar 1994).

2.3.3 Multiple predators

To study the effects of multiple predators (weasel, owl) on population growth of field and sibling voles and the possible effects of intraguild predation on the predation efficiency of the least weasel (chapter V), experiments were conducted in 2007. Because of logistic restrictions, the treatments with weasel predation only and the combined predation of a weasel and an owl could not be executed simultaneously. Therefore, the combined predation treatment (weasel and owl, WO) was conducted first, and the weasel only (W) treatment directly thereafter. At the start of the WO treatment at the end of August 2007, 30 individuals (18 females and 12 males) of both field voles and sibling voles were released into each of the four enclosures (1 ha). The voles were released at the gate separating the two sub-enclosures to allow the voles to disperse to both areas. Five days later one male weasel, and a day after that one female Tengmalm's owl, was released into each of two enclosures (WO treatment). The two remaining enclosures acted as controls (C). The predators were allowed to move and hunt freely inside the enclosure for three weeks. After the end of the treatment, vole populations were live-trapped.

The least weasel only treatment (W treatment) was initiated at the end of September by releasing one weasel into two 1 ha enclosures with the two remaining enclosures as controls. The vole populations had been undisturbed after the trapping at the end of the WO experiment. After three weeks the weasels were removed from the enclosures and the vole populations again monitored by live-trapping.

2.3.4 Laboratory experiment

A laboratory experiment was conducted to test the predation risk allocation hypothesis of Lima and Bednekoff (1999) using least weasels and field voles as a model system (chapter IV). The experiment was carried out in 0.5 × 0.5 m arenas fenced with 0.8 m high hardware cloth, with 0.2 m wide metal sheets on the top of the fence to prevent the escape of voles. The arena floor was covered with a grid of Petri-dishes (diameter ca 3 cm) screwed to the floor in 4 rows of 5 dishes. Each trial consisted of a habituation period lasting from the beginning of the trial until noon of the second day, and an actual 2 h experimental period in the end of each trial. During an experimental trial one oat seed was put into each of the 20 dishes five times (on day 1 at 11.30 and 15, on day 2 at 8, 11.30 and 13.30). The measure of the amount of foraging activity during the experimental period (on day 2, between 11.30 and 13.30) was the number of seeds removed from the Petri-dishes.

High risk situations (α_H) were simulated by exposing voles to the presence of a least weasel (treatments with a high attack ratio) or its fresh faeces (treatments with a low attack ratio). During the low risk situations (α_L) no stimulus indicating risk of predation was present. The proportion of time at high risk was manipulated by using high-risk periods lasting from 10 minutes to 5.5 hours. In the treatments with low proportion of time at high-risk, voles were exposed to least weasel or its faeces for 10 minutes during the first day and for two hours during the second day. In the treatments with high proportion of time at high-risk, vole were exposed to weasel or faeces for 3.5 hours on the first day and 5.5 hours on the second.

In the treatments where voles were exposed to the presence of a live least weasel, a weasel nest box (sides 0.5 × 0.5 m, height 0.45 m) was installed next to the feeding arena of voles. The weasel was able to exit the nest box and enter a plexi-tube (diameter 0.1 m), which passed through the feeding arena of voles. The tube had holes (diameter 0.01 m) on both sides, which allowed weasel odour and vocalizations to penetrate into the vole arena. In the treatments with weasel faeces a similar part of tube with fresh weasel faeces inside crossed the vole arena. An empty clean tube was used in control treatments.

2.4. General methods

2.4.1 Live-trapping

Each year, before the beginning of the field experiments, all rodents were removed from the enclosures and controls using both live-capture and snap traps. The trapping was continued uninterrupted until no rodents were captured for two or three consecutive days. Vole population growth was monitored by live-trapping on several occasions each year, usually from the end of May to September-October using standard capture-mark-recapture–techniques. The time period between trappings was between two and three weeks. Two of the study sites were trapped first for three days and then the other two sites for a further three days. Traps were baited with Rat/Mouse Breeding Diet pellets (Altromin GmbH, Germany) and checked three times per day, in the morning (at 6:00), in the afternoon (14:00) and in the evening (21:00). Voles were marked individually, weighed with a spring scale (Pesola AG, Swizerland, accuracy ±1 gram), sexed, and their current reproductive status was noted based on external appearance. Other rodents, bank voles, harvest mice (*Micromys minutes*) and house mice (*Mus musculus*), that occasionally occurred in the traps were removed from the enclosures.

During live-trapping the current reproductive status of each vole (males: submature/mature/postmature, females: submature/mature/gravid/lactating/postmature) was noted. A vole was classified postmature if it reproduced during summer but ceased breeding due to the onset of winter. For the estimation of reproductive parameters, voles were classified as young or adult by body mass. Individuals weighing 15 g or less were defined as young and all above that as adults (Innes and Millar 1994, Myllymäki 1977b). The reproductive status of adult voles was classified as either active (mature/gravid/lactating) or inactive (submature/postmature) (chapter I).

Population density estimates for voles were calculated from trapping data using the jackknife estimator for model M_h in the program CAPTURE (Otis et al. 1978). Estimates were separately calculated for each species, enclosure and trapping session.

2.4.2 Predators

The least weasels used in the field experiments in 2005 (chapter II) and 2007 (chapter V) were either wild-caught from Lapua and surroundings or from a breeding stock at the Konnevesi research station (University of Jyväskylä). The weasels were kept in cages (120 x 60 x 60 cm) from two to five weeks before the experiments and fed with dead voles and mice. The least weasels were radio-collared in order to follow their movements in the enclosures and to facilitate recapture of the animals. Radio-collars (type TW-4, Biotrack, UK, weight ca. 3.2 g) were fitted under full anaesthesia (inhalant isoflurane) 1-2 days before release to allow time for the animals to get accustomed to the collars. Weasels were weighed and sexed by external appearance (Brandt and Lambin 2005). In 2005 three radio-collared weasels were released into three randomly chosen enclosure sections (0.5 ha), one in each, and in 2007 one weasel into two whole enclosures each (1 ha). Both male and female least weasels were used in 2005, whereas in 2007 all weasels were males.

In 2007 also two female Tengmalm's owls with radio-transmitters were released into the same enclosures as the weasels (chapter V). The owls were kept in an outdoor aviary until the start of the experiment and fed with dead voles and chickens. Prior to the experiment, the owls were fitted with radio-transmitters (type TW-4, Biotrack, UK, weight ca 3.2 g) that were attached to 2-3 tail feathers using a combination of glue and sewing thread a couple of days before the treatment started. Male weasels and female owls were chosen in order to avoid large differences in size (body masses of 68 g and 88 g for the two least weasels and 149 and 170 grams for the two owls), thereby minimizing the risk of potential for intraguild predation. Reviews of intraguild predation among mammalian and avian predators show that the predator species is usually three times larger in body mass than the victim species (Palomares and Caro 1999, Sergio and Hiraldo 2008).

3. Results and discussion

3.1 Competition

3.1.1 Demographic parameters

The competition experiment (I) was conducted in order to study the effects of a coexisting species on the population growth of field and sibling voles. I found that population densities of both vole species were lower in the presence of the other, so coexistence was apparently deleterious to both of them. However, the effects of competitors were greater for field voles, which thus seemed to suffer more from the presence of coexisting species than sibling voles. Therefore, on a population level, sibling voles were found to be superior competitors in the absence of predators, due to better survival and possibly to greater reproductive capability.

The main difference between these two very similar species lies in their sociality: sibling voles tend to live at higher local densities than field voles (Norrdahl and Korpimäki 1993). The common vole (*Microtus arvalis*), which is a very close relative of the sibling vole, and which coexists with the field vole in central and western Europe, is known to reproduce in family groups (Boyce and Boyce 1988a, b, c), but it is not known if the sibling vole has a similar reproductive system. Dense colonies of sibling voles may be able to monopolize local habitats and exclude potential interspecific competitors, i.e. field voles (Norrdahl and Korpimäki 1993). Since space, and therefore also food, are limited in the enclosures (e.g., Klemola et al. 2000, Huitu et al. 2003), competition is bound to increase at high densities. Persson (1985) suggests, contrary to the usual expectation, that in some situations (e.g. when food is scarce) smaller species can actually have a competitive advantage over larger ones, because of their lower food requirements. Nevertheless, on an individual level (interference competition), the smaller sibling voles are probably not able to exclude field voles from preferred areas. Thus their competitive superiority is most likely based on a more aggregated way of life, which gives them advantage through numbers (exploitation competition), but also makes them more vulnerable to predation (Norrdahl and Korpimäki 1993). Since greater competition for food likely occurs in winter than in summer (Huitu et al. 2003), the competitive superiority of sibling voles may be even more pronounced during winter.

3.1.2 Habitat use

In the same experiment where the impact of competition on population growth was studied (I), I also examined the effects of interspecific competition, population density and predation risk by the natural predator guild on habitat selection (short vs. tall grass) (III). The scenario in which individuals should be most free to select their preferred microhabitat involves low to moderate intraspecific densities, no interspecific competitors and no risk of predation. Under these circumstances sibling voles used short grass habitat to a lesser extent than did field voles (III). This is unexpected, since sibling voles are suggested to use short grass habitats more than field voles (Myllymäki 1977a, Norrdahl and Korpimäki 1993). However, these earlier observations are from natural surroundings where the two species are rarely, if ever, alone or free from the risk of predation. Based on my results, it is possible that sibling voles do not prefer short grass habitat in the wild, but rather use it more due to competition with field voles, either voluntarily or following exclusion by field voles. Even though sibling voles are superior competitors at the population level (I), interspecific interactions may have different outcomes at an individual level. In a similar case, Ziv et al. (1993) found Egyptian sand gerbils to force Allenby’s gerbils to less preferred habitat type, even though Allenby’s gerbils were about twice as likely to be caught in the favoured habitat at low densities and in the absence of Egyptian sand gerbils (Abramsky et al. 1990).

In the absence of interspecific competitors and predators the proportion of short grass habitat used by sibling voles increased with population density. Similarly, the proportion of meadow voles in mowed habitat correlated positively with density (Pusenius and Schmidt 2002). Also Löfgren (1995) found that for all species studied, the bank vole, the grey-sided vole (*Myodes rufocanus*) and the field vole, the breadth of the habitat niche increased with increasing density. Field voles living in a competitor- and predator-free environment utilized short grass habitat relatively more than sibling voles at low densities. However, their use of short grass decreased as population densities increased. A simulation analysis of Hansson (1995) showed that the niche of some predator species contracted in response to intraspecific competition, and that this contraction was more common at high competition intensity. This model can be applied also to my results; field voles might have favoured certain plants (e.g. timothy; see Norrdahl et al. 2002) that were abundant in the mowed area when vole densities were low. When densities grew, the supply of preferred plants may have been exhausted (see Norrdahl et al. 2002), which could have lead to niche contraction (Hansson 1995). Changes in the plant community have been suggested as a cause for the earlier cessation of the reproductive season of field voles compared to sibling voles (so called midsummer crisis, Myllymäki 1977b); field voles reproduce most efficiently in early summer, whereas sibling voles do so in late summer (Norrdahl and Korpimäki 1993, I).

Under coexistence at low or moderate densities in the absence of predation, the two species behaved as previously described (Myllymäki 1977a, Norrdahl and Korpimäki 1993): sibling voles used the short grass habitat proportionally more than field voles. However, the difference became less pronounced with increasing densities. The response of field voles is one that is often documented: niche contraction at low densities in response to interspecific competition (e.g. Eccard and Ylönen 2002), which seems counterintuitive. Perhaps field voles opt for safer, tall grass habitats because patches of sibling voles lure more predators (apparent competition, Holt 1977). Sibling voles, on the other hand, had broader niches at low densities, as indicated by a greater proportion of short grass use. At higher population densities the relative use of high grass approached that of field voles. This phenomenon may be due to changes in the relative size of different functional groups within the species. Because the proportion of young voles in sibling vole populations is higher than in field voles, increasing densities may be synonymous to an increase in the number of young voles that exhibit greater tolerance in respect to competition for habitat (e.g. Ostfeld 1986).

3.2 Predation

3.2.1 Risk allocation

The results of the laboratory experiment (IV) testing the predation risk allocation hypothesis (Lima and Bednekoff 1999) demonstrated the importance of temporal variation in predation risk as a factor affecting foraging decisions of field voles. Results indicated that the feeding effort allocated to low vs. high risk situations depended on the relative degree of risk in high-risk situations, i.e. the attack ratio. Voles also seemed to exhibit their greatest antipredatory behaviour during brief high risk situations. Thus, the findings agreed with some of the key predictions of the predation risk allocation hypothesis of Lima and Bednekoff (1999). However, no clear evidence of changes in feeding effort was observed in relation to variation in the proportion of time spent at high-risk situations. In addition, the fit between the observed values of feeding effort and the values predicted from the model of Lima and Bednekoff (1999) was only moderate. The actual presence of a weasel caused a clear decrease in foraging activity of voles, whereas weasel scent caused only mild effects. The presence of scent alone indicates that a weasel has been around but the chance that it will come back may not be great. In fact, the levels of feeding activity after the weasel had visited corresponded with those measured in the presence of scent.

Although the greatest decrease in feeding effort occurred during a brief exposure to a live weasel, the feeding effort during the longer weasel exposure was not much higher than during the shorter one. Perhaps the trials were too short to cause any changes in the nutritional condition of the voles. However, the decrease in body mass of voles during the trials with the highest p values and attack ratios (no decrease during the other trials), suggests that voles began to suffer from malnutrition in the prolonged presence of weasel (see also II). Thus, they should have been motivated to take risks in order to retain their energy balance. Probably voles, housed in the laboratory for an extended period, had initially a highly favourable energy balance (e.g. Unangst and Wunder 2003).

The results seem to be similar with those of Van Buskirk et al. (2002). They exposed tadpoles to their dragonfly larvae predators, and found increased vigilance at high risk situations as attack ratio increased, but did not detect any effect due to variation in p. The results of Hamilton and Heithaus (2001) and Sih and McCarthy (2002) with snails and their crustacean predators indicated increased foraging activity of prey associated with high p. Thus, the occurrence of the phenomena predicted by Lima and Bednekoff (1999) may depend on the system studied.

3.2.2 Least weasel predation

Exposure to freely-hunting least weasels for three weeks affected population densities of both vole species negatively (II). However, the effect was more pronounced in sibling voles in which population densities decreased markedly during the treatment period and even after that. These results imply that predation by a least weasel can not only suppress local populations of sibling voles but also affect their dynamics beyond the time of predator presence.

The population mean body mass of both vole species decreased during exposure to weasel, which suggests that weasels selectively preyed on larger and energetically more profitable, individuals (see Sundell and Norrdahl 2002). The smallest voles can also use burrows that are too small for weasels to enter, offering them refugia from weasels (Sundell and Norrdahl 2002). However, the mean mass of those sibling voles trapped both before and after the weasel treatment also decreased. Predation risk is known to affect the movements and feeding behaviour of voles, which can in turn lead to a decline in mass of the animal, at least in the laboratory (Carlsen et al. 1999, IV). On the other hand, smaller size in some animals can act as an antipredatory defence (Gosler et al. 1995). Thus weasels may have both selectively hunted heavier voles and had indirect negative effects on the body mass of voles.

There was no obvious difference between the control and treatment populations in the measured reproductive parameters of voles. Predators are thought to suppress breeding in voles, but the results supporting the hypothesis are mainly from laboratory experiments (e.g. Ylönen 1989, but see Fülling and Halle 2003) in which predation risk is often presented as short-term pulses within periods of apparent safety (Mappes et al. 1998). This scenario may be very different from the type of risk perceived by voles in nature. Of course, the effects in my experiment could have been too small to detect or occurring at a low rate on an individual level and, therefore, not cumulatively expressed on a population level. Survival of females was lower in treatment than in control populations in both species, however. Mammalian predators tend to remove more female than male voles from the population (Norrdahl and Korpimäki 1998), which will ultimately have negative effects on vole population growth.

3.2.3 Multiple predators

The effects of multiple predators, least weasel and Tengmalm's owl, on population densities of field and sibling voles were studied in paper V. The presence of Tengmalm's owl clearly decreased the impact of a smaller predator, the least weasel, on vole populations (V). Population densities of sibling voles were higher following exposure to both weasels and owls, as compared to exposure to weasels only. Densities of both vole species were significantly lower after exposure to weasels only compared to controls. These results suggest that the potential for intraguild predation between owls and weasels may have caused a reduction in predation risk, especially for sibling voles. Such a reduction in risk could result from two related mechanisms. First, weasels could respond to the increase in predator density itself and not the other predator species *per se*. Second, weasels could respond to risk of intraguild predation risk (Polis et al. 1989, Polis and Holt 1992, Holt and Polis 1997, Sih et al. 1998). The presence of an owl could indeed cause a behavioural change in weasels, such as a reduction in activity levels. Decreased activity levels in weasels and possibly also in voles would lead to fewer encounters between the species, which should decrease the hunting efficiency of the weasel.

Sibling voles were competitively superior to field voles on a population level when they are not exposed to predation (I), but inferior when preyed upon by weasels (II). This suggested that weasel predation may play an important role in shaping the competitive relationship between these two species, which was in this experiment (V) supported. However, in nature the communities of both prey and predator consist of multiple species which may interact in various ways, making generalization of my results difficult. Least weasels are found in small numbers in the diets of avian and larger mammalian predators, in particular in the decrease phase of the vole cycle (Korpimäki and Norrdahl 1989, Dell'Arte et al. 2007) which suggests that intraguild predation may have negative effects on the hunting efficiency of weasels, which may, in turn, greatly influence community composition.

3.3 Effects of predation on competition

3.3.1 Facilitation of coexistence

Predation reduced the abundance of sibling voles more than that of field voles (II, see also V). Therefore, predation reduced the strength of interspecific competition for both vole species, but particularly so for field voles. These results are in general agreement with previous studies carried out with other taxonomic groups (reviewed by Sih et al. 1985, Gurevitch et al. 2000): predation reduces the strength of interspecific competition and thereby reduces the likelihood of competitive exclusion (e.g. Paine 1966, Vance 1974, Crowley 1979).

Least weasels could be promoting coexistence of the vole species via two mechanisms. First, weasels may merely select the more aggregated species, in this case the sibling vole, as prey (Murdoch and Oaten 1975, Roughgarden and Feldman 1975, Sundell et al. 2003). Second, if population growth rate is a reflection of the competitive ability of a species, and there is a trade-off between this ability and predation resistance (Vance 1974, Lubchenco 1978, Leibold 1996), sibling voles may simply be more vulnerable to weasel predation than field voles. This vulnerability can be due to, or accentuated by, the tendency of sibling voles to form dense aggregations (Norrdahl and Korpimäki 1993). Although aggregation can in some cases decrease predation risk (e.g. Turchin and Kareiva 1989), this is not uniformly so. For example, Kondoh (2003) suggested that the more clustered spatial distribution of the superior competitor in fact increases vulnerability to predation (see also Connell 2000). Because weasels are efficient predators that may kill more than they eat (Oksanen et al. 1985), their impact on high-density prey patches may be severe.

3.3.2 Habitat use

Predation risk together with interspecific competition reduced the use of short grass habitat in sibling voles (III). In particular, at higher densities sibling voles were not encountered in the short grass area at all, which is again in stark contrast to earlier accounts of sibling vole habitat preferences (Myllymäki 1977a, Norrdahl and Korpimäki 1993). Either sibling voles reacted to a perceived risk of avian predation by staying in cover, or those voles that did use short grass were selectively hunted from the population. By contrast, field voles under interspecific competition used very little short grass to begin with, so there was little need for them to shift habitat in response to avian predation risk. While the use of tall grass might be effective against avian predators, it may predispose voles to small mustelids hunting under cover (Korpimäki and Norrdahl 1989, Brandt and Lambin 2007). However, voles appear to regard avian predators a bigger threat than mammalian predators, and commonly respond more strongly to risk of the former (Korpimäki et al. 1996).

Although both vole species preferred tall grass (safer, but poor) habitat over short grass (risky, but productive) habitat, they pronouncedly aggregated in the former at high densities while under predation risk. Of the two *Microtus* species, sibling voles are presumable the preferred prey of mustelids (see II and V), which hunt under tall vegetation, as well as avian predators hunting in more open areas (Norrdahl and Korpimäki 1993). Thereby, it is possible that the ratio of predation risk between tall grass and short grass habitats is lower for sibling voles than for field voles. If this were the case, these results support the predictions of Grand and Dill (1999): sibling voles, which are superior competitors (I) and have a lower risk ratio across short and tall grass habitats, aggregated together with field voles in the nutritionally poorer, but safer, tall grass as predation risk became diluted with increasing population densities. However, the actual risk ratios of the two vole species are not known, and also the competitive interactions between the species require further study.

4. Conclusion

These are the first experimental results on the interspecific interactions between two highly similar small mammal species, sibling voles and field voles. My results show that the sibling vole is indeed the superior competitor in the absence of predation (I), but on the other hand more vulnerable to predation (II, V). Since sibling voles were unable to extirpate field voles from any of the enclosures during the competition experiment even in the absence of predation (I), it is not likely that they would be able to displace field voles in predator-free natural surroundings either. Despite the competitive superiority of sibling voles, field voles are generally more numerous in nature in our study area (Huitu et al. 2004). This alone indicates that predation most likely has a profound influence on the interspecific dynamics of these two species, and hence community composition (Norrdahl and Korpimäki 1993). The results from the predation experiments (II, V) show that predation has a greater negative impact on an apparently superior competitor (i.e. the sibling vole) than on a subordinate one. In effect, predation alleviated interspecific competition between the vole species and is, therefore, a potential factor enabling their coexistence.

Coexistence might also be promoted by niche differentiation. Field and sibling voles coexist in seemingly similar habitats side by side in many areas, also at spatial scales of some tens of meters. Sibling voles have been previously suggested to prefer shorter grass habitats more than field voles do (Myllymäki 1977a, Norrdahl and Korpimäki 1993). Results of the habitat selection experiment (III) clearly indicate that patterns such as these observed under natural conditions cannot be interpreted solely as a result of interspecific interactions but must also include the effects of predation risk. When vole densities increased to the level of peak densities of vole cycles (ca. 200 individuals per hectare, e.g. Korpimäki et al. 2004), differences in habitat selection attributable to interspecific competition and predation tended to disappear (III). Therefore, coexistence of the two species cannot be explained by temporally consistent differences in habitat selection. However, persistence of coexistence may be mediated by habitat selection at low population densities, which coincide with periods of predator scarcity.

The importance of predation on population fluctuations of voles has been under debate for a long time (e.g. Henttonen et al. 1987, Batzli 1996, Jedrzejewski and Jedrzejewska 1996, Korpimäki and Krebs 1996, Krebs 1996, Hanski et al. 2001, Oli 2003, Korpimäki et al. 2003, 2005b). The results of the weasel predation experiment (II) showed clearly that predation by least weasels can suppress vole populations locally even during summer under abundant food conditions. Moreover, the effects persist even after the predator has vacated the area. In addition to hunting, weasels can also affect populations of their vole prey indirectly (II, IV). Reduction of feeding can cause a decline in the physical condition of a vole and make it therefore more vulnerable also to diseases or predation (Huitu et al. 2007, Beldomenico et al. 2008). What is more, poor body condition can also reduce the success of a vole in competitive interactions. Timing foraging to the short periods of lower risk (IV) might be difficult when predation risk is imposed by multiple predators (V). However, the hunting efficiency of least weasels can be limited due to predation risk from owls, leading thus to risk reduction in voles (V).

The natural predator community is a complex assemblage of various types of predators. The behaviour of those predators which prey on least weasels can also be altered by other, larger predators. For example, the presence of red fox can decrease activity levels of stoats, which in turn can reduce predation pressure on least weasels (mesopredator release, e.g. Sih et al. 1985, Courchamp et al. 1999). The composition of the predator guild varies temporally (seasonally as well as between day and night), which can cause the actual predation pressure on voles to vary accordingly. A decrease in predation efficiency by one species of predator type can lead to compensation by another (Korpimäki and Norrdahl 1998, Norrdahl and Korpimäki 1995). Therefore to fully understand the boreal grassland ecosystem consisting of multiple vole species as well as their multiple predators, we need to know more about the interactions between different kinds of predators and how the outcomes of those interactions cascade on shared prey and even to lower levels of grassland ecosystem, the food plants of voles.

Sibling voles appeared in Finland probably no earlier than in the 1940's (Sulkava and Sulkava 1967), so the competitive situation between these two species in the study area is relatively new. Intentionally or unintentionally introduced species can have detrimental effects on ecosystems. While alien predators are probably the best known examples of such introductions (e.g. Gurevitch and Padilla 2004, Salo et al. 2007, Banks et al. 2008, Fey 2008) also herbivores can cause various problems, such as harming the native flora and competing with native herbivores (Donlan et al. 2002). Most introduced species, however, are not able to establish self-sustaining populations (Williamson and Fitter 1996). Successful establishers are usually, e.g., superior competitors and able to occupy vacant niches. Apparently the sibling vole possesses these abilities, since it has been capable to settle not just in Finland, but also elsewhere, for example on the isolated island group of Svalbard (e.g. Frafjord 2002). Because of global warming, we can expect more new species, both herbivores and predators, expanding their distribution especially towards boreal and arctic regions (e.g. Parmesan 2006). Since our understanding of the complex interactions within ecosystems even in their current state is limited, the future will bring great challenges for researchers in biological sciences.

Small mammals are prime model species for testing ecological theories, e.g., because of their small size, which makes large-scale experimentation possible. Since basic mechanisms underlying processes of population dynamics are universal, i.e., consisting of four demographic variables, reproduction, mortality, immigration and emigration, results obtained from different species and ecosystems should readily be applicable to others. For example, the plains of Africa contain an even more complex assemblage of prey and predator species than boreal grasslands (see e.g. Owen-Smith and Mills 2008). Understanding the complicated interactions between such species is essential for the conservation of endangered and threatened species, for instance in savannah or rainforest ecosystems. However, the holistic understanding of complex ecosystem processes cannot be achieved without smaller steps, for example the experimental dissection of interaction processes occurring in simpler systems.

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