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**DETRIMENTAL EFFECTS
OF ALIEN MINK PREDATION
ON SMALL MAMMAL POPULATIONS
AND CASCADING EFFECTS ON PLANTS
IN THE BALTIC SEA ARCHIPELAGO**

by

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Was denkt die Maus am Donnerstag,
am Donnerstag,
am Donnerstag?

Dasselbe wie an jedem Tag,
an jedem Tag,
an jedem Tag.

Was denkt die Maus an jedem Tag,
am Dienstag, Mittwoch, Donnerstag,
und jeden Tag,
und jeden Tag?

O hätte ich ein Wurstebrot
mit ganz viel Wurst und wenig Brot!
o fände ich, zu meinem Glück,
ein riesengrobes Schinkenstück!
Das gäbe Saft, das gäbe Kraft!
Da wär ich bald nicht mehr
mäuschenklein,
da würd ich bald groß wie ein Ochse
sein.
Doch wäre ich erst so groß wie ein
Stier,
dann würde ein tapferer Held aus
mir.
Das wäre herrlich,
das wäre recht -
und ~~der Katze~~ dem Mink,
~~der Katze~~ dem Mink
ginge es schlecht!

Josef Guggenmos

This thesis is based on the following publications and manuscripts, referred to in the text by their Roman numerals:

- I** Fey K, Banks PB, Korpimäki E (2006): Different microhabitat preferences of field and bank voles under manipulated predation risk from an alien predator. - *Annales Zoologici Fennici* **43: 9-16**.
- II** Fey K, Banks PB, Ylönen H, Korpimäki E: Behavioural responses of voles to simulated risk of predation by a native and an alien mustelid: an odour manipulation experiment. – *Submitted manuscript*.
- III** Fey K, Banks PB, Korpimäki E: Voles on small islands: effects of food limitation and alien predation. – *Submitted manuscript*.
- IV** Fey K, Banks PB, Korpimäki E: Alien mink predation impedes colonisation processes of voles on small islands of the Baltic Sea – *Submitted manuscript*.
- V** Fey K, Banks PB, Oksanen, L, Korpimäki E: Does removal of an alien predator from small islands in the Baltic Sea induce a trophic cascade? – *Submitted Manuscript*.

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1. INTRODUCTION

As humans have spread around the globe, they have intentionally or accidentally transported a huge variety of plant and animal species to locations beyond their natural range (Elton 1958; Williamson 1996; 1999). The earliest evidence of the introduction of non-indigenous species dates back to the Neolithic era, c. 6000 BP (Webb 1985). The colonization of Hawaii by Polynesians c. 1000 BP and other prehistoric human movements were soon connected with the introduction of new species and the extinction of local ones (Olson and James 1982; Manchester and Bullock 2000; Burney et al. 2001). It was, however, not until the 16th century, when marine transportation improved and the rise of the European colonial expansion caused massively increased human movements between continents, that introductions became more frequent (Elton 1958; di Castri et al. 1990; Leppäkoski et al. 2002). Since then they have continued to increase; many hundreds of introduced species have established self-sustaining wild populations and have caused dramatic changes in many ecosystems worldwide (Gurevitch and Padilla 2004). While some species were intentionally introduced (e.g. the water hyacinth *Eichhornia crassipes* or the Nile perch *Lates niloticus* to Lake Victoria, Africa), others stowed away on aircrafts or ships (e.g. the agent of avian malaria, *Plasmodium relictum*, to Hawaii, the brown tree snake *Boiga irregularis* to Guam, or the rat *Rattus rattus* to Polynesia); yet other invaders have been escaped or released domestic animals (e.g. the feral cat *Felis catus* in Australia or the feral pig *Sus scrofa* in many parts of the world). The damage done by these species now offers infamous examples of how devastating the impact of an alien species can be (Lowe et al. 2000).

Not all introduced species are able to establish self-sustaining populations. For a majority of plants and animals the “rule of tens” holds: one in ten imported species appears in the wild, one in ten of those introduced becomes established, and one in ten of those established becomes a pest (Williamson and Fitter 1996a). The factors that determine whether or not a species is a successful invader include both species traits and ecosystem properties (Williamson and Fitter 1996b; Williamson 1999). Successful invaders are usually opportunistic, superior competitors and able to settle in empty niches in their new environment. In addition, they often benefit from the absence of competitors, predators and parasites in their new environment. Their ability to invade depends also on the physical environment and resource availability (Shea and Chesson 2002).

1.1 Introduced predators

The negative impact of alien species on the native fauna may be caused directly through three processes: predation, competition, and the transmission of disease, parasites or pathogens to native species (Dickman 1992b; 1996). Indirect effects may occur at the community level via effects on keystone species (Spiller and Schoener 1994). Among these processes, alien terrestrial predation is considered to have the worst effect on native species (Diamond 1984). Predation by introduced predators has

been the cause of some of the most rapid and severe changes in native bird and mammal populations all over the world.

Probably the most notorious example is the introduction of brown tree snakes (*Boiga irregularis*) to the island of Guam in the Western Pacific Ocean. Within a few decades of the arrival of brown snakes, Guam lost all but three of its thirteen native bird species and several bat and reptile species (Fritts and Rodda 1998). In Australia, the introduction of cats (*Felis catus*), red foxes (*Vulpes vulpes*) and dingos (*Canis lupus dingo*) is linked to the extinction of several species of mammals, birds and tortoises (Dickman 1996). Extinctions are also known in less charismatic taxa, such as the extinction of tree snail species on the Hawaiian islands caused by a North American predatory snail, *Euglandina rosea* (Hadfield et al. 1993).

In addition to global extinctions, many species have become locally extinct, are threatened, or have severely declined. Since alien predators are usually generalists, it is easily possible for them to exterminate a prey species without exhausting their potential food supply (Diamond 1989).

In co-evolved predator-prey systems, the mere risk of predation can induce behavioural changes in potential prey which are assumed to reduce the risk of being killed by a predator. These include changes in activity patterns, the use of home ranges and habitats, foraging and even reproduction patterns (Lima and Dill 1990; Kats and Dill 1998). In mammalian predator-prey systems, efficient perception of predation risk is often based on residual olfactory cues; this favours avoidance of predators early in the sequence of predator-prey interaction (Kats and Dill 1998; Apfelbach et al. 2005).

Without a long history of coexistence with a comparable predator, however, native prey may not be able to recognise alien predators as dangerous (level 1 naïveté), or they may lack the appropriate anti-predatory responses (level 2 naïveté) (Banks and Dickman 2007). It is this phenomenon that is thought to lie behind the especially pronounced negative impact of alien predators in simple systems such as oceanic islands or archipelagos, since these are usually predator-free systems or have only a few ground-living mammalian predators (Atkinson 1985; Dickman 1992a; Atkinson 1996). Moreover, dispersal and re-colonization rates in island systems are low, so that losses to alien predation can not be redressed by immigration (Tamarin 1978; Peltonen and Hanski 1991; Adler and Levins 1994). In a recent world-wide review of predator-removal experiments, Salo et al. (2007) showed that the impact of alien predators was indeed worst in insular ecosystems, provided that Australia was considered an island; this is reasonable given Australia's unique evolutionary history.

The relationship between an introduced predator and a native prey, however, may have several different outcomes (Ebenhard 1988; Dickman 1996). The one most often observed is the severe decimation or extinction of the prey species. But if the predator population is small, or if for instance only juveniles are predated while breeding animals are unaffected, the effect of alien predation on the native prey population may be minor (Banks 1999). If interactions occur among introduced predators and other exotic species, the negative effects on prey populations may be more pronounced or on

the contrary diluted (Zavaleta et al. 2001). In some cases, predation may have a positive impact on prey populations. On small islands, for example, high herbivore densities are often promoted by the absence or low densities of predators and limited dispersal (the so called "fence effect"; Boonstra and Krebs 1977; but see Ostfeld 1994). Overexploitation of food resources is often the main cause of population crashes or complete extinction of island populations (Pokki 1981). If predators enter such island systems, they may prevent the complete extinction of their prey populations by limiting herbivore numbers before they completely exhaust their resources (Wilmers et al. 2006); this on the other hand removes the motivation for dispersal and thus interrupts meta-population processes. Information on the causes of extinctions and threats due to alien predators, however, is in many cases anecdotal, speculative or based on limited field observation (Williamson 1996; 1999).

It is also possible for alien predation to have an impact throughout a whole ecosystem. Changes in predator abundance, by altering the abundance of herbivores, can modify the distribution and abundance of plants on a community-wide basis, an effect known as a trophic cascade (Carpenter et al. 1985). Trophic cascades have been shown to occur following the removal of predators preying upon herbivores (Schmitz et al. 2000; Norrdahl et al. 2002), but there is still disagreement as to whether community-level trophic cascades might be widespread and strong in terrestrial ecosystems (Polis and Strong 1996; Polis et al. 2000; Schmitz et al. 2000). A cross-ecosystem comparison of the strength of 102 trophic cascade experiments showed that plants in aquatic ecosystems responded more strongly to predator reductions than those in terrestrial ecosystems (Shurin et al. 2002). The issue, however, is debated, and some authors maintain that trophic cascades also commonly occur in vertebrate terrestrial food webs (Oksanen and Oksanen 2000; Terborgh et al. 2006; Aunapuu et al. 2008), which are greatly under-represented in the material underlying the recent meta-analyses (Halaj and Wise 2001; Shurin et al. 2002; Borer et al. 2005; Shurin et al. 2006). Possible reasons for the rarity of community-level trophic cascades in terrestrial systems include self-regulation or abiotic limitation of herbivores and the diversity of defense strategies in plants (Polis 1999; Schmitz et al. 2000). The main reason, however, may be the architecture of high-diversity terrestrial ecosystems, which forms a complex web rather than a simple chain (Polis 1991). Island ecosystems are usually simpler systems with a more chain-like structure, thus having greater potential for trophic cascades. Moreover, biodiversity is usually lower on islands than on the mainland. Herbivore populations on small islands often have high densities, since they suffer little or no predation. In addition, they have limited dispersal; thus the so-called fence effect may lead to abnormally high population growth (Boonstra and Krebs 1977; but see Ostfeld 1994). Thus overgrazing can have a widespread impact on island plant communities.

Herbivores affect the structure and diversity of plant communities by reducing the abundance of preferred forage species and by modifying competitive interactions between plant species (Whitham et al. 1991). It is not clear, however, whether plant communities benefit from a drastic reduction of herbivores. Plant diversity may be positively influenced by disturbance, which prevents competitive exclusion by creating resources for subordinate species (Connell 1978; Mack and D'Antonio 1998; Kondoh

2001). If so, predation may not only limit prey populations, but also reduce the biodiversity of communities and whole ecosystems.

A worldwide meta-analysis of the responses of vertebrate prey in field experiments in which the population densities of mammalian and avian predators had been manipulated showed that alien predators had a suppressive impact on prey which was double that of native predators (Salo et al. 2007). This finding in turn suggests that alien predators may induce stronger trophic cascades in plant communities than do native predators. However, there are no previous experimental studies on possible trophic cascades induced by alien predators.

1.2. Predator removal experiments

Removing predators has turned out to be a convenient method for revealing the effects of predation on prey populations (Sih et al. 1985; Korpimäki and Norrdahl 1998; Korpimäki et al. 2002; Korpimäki et al. 2005). Unlike predator exclusion for instance by nets or fences, in predator removal experiments prey populations are not influenced by any other factor than the presence or absence of the predator in question. Permanent removal of vertebrate predators on a landscape scale, however, is almost impossible, except perhaps for isolated islands (Myers et al. 2000).

The outcomes of large-scale predator removal experiments may be affected by at least three important mechanisms. First, it may be extremely difficult to remove all individuals of a predator species (Zavaleta et al. 2001). Moreover, in the absence of intra-specific competition for resources, remaining or re-colonising predator individuals may show increased reproductive success and/or survival. This may lead to an actual increase in the predation rate compared to pre-removal conditions (Boyce et al. 1999). The predator population may also be quickly restored by dispersing individuals from the surroundings (Byrom 2002; Korpimäki et al. 2002). Continuous and year-round removal is thus essential; otherwise the predator reduction period will remain short. Second, if only one predator species is removed, the remaining predators may increase their predation rate or shift their diet, which will dilute the effect of removal (Norrdahl and Korpimäki 1995; Korpimäki and Norrdahl 1998). Finally, reduced predation pressure may lead to an increase in both intra- and inter-specific competition among prey individuals, and a stronger competitor may start to dominate the system (Paine 1966; Henke and Bryant 1999).

Thus islands and insular systems, which generally have fewer predator species and slower re-colonisation rates than mainland habitats, are well suited for large-scale predator removal, since the effects of predator removal may be more distinct there (Marcström et al. 1988; Côté and Sutherland 1997; Macdonald et al. 2002).

1.3 Aims of the thesis

The American mink (*Mustela vison*, hereafter mink), is a medium-sized mustelid which since the first half of the twentieth century has been transported far beyond its

native range in North America for purposes of fur farming. Through accidental escapes or deliberate releases mink have become established in semi-aquatic ecosystems of Northern and Eastern Europe, including archipelagos and the British Isles (Bonesi and Palazon 2007). Almost everywhere it has been introduced, the mink has been suspected of having a notable negative impact on some of its prey species. One such case is the dramatic decline of water voles (*Arvicola terrestris*) in the U.K. (Woodroffe et al. 1990; Aars et al. 2001; Macdonald and Harrington 2003). The effect of mink on water voles in the U.K. is confounded by the post-war intensification of agriculture that has led to the destruction of riverside and flood plain habitats, but mink has also been shown to limit water vole populations in unmanaged wetland systems in Belarus (Macdonald et al. 2002). There is concern over mink impact on ground-nesting birds in the U.K. (Ferrerias and Macdonald 1999; Moore et al. 2003), Poland (Bartoszewicz and Zalewski 2003), and the mainland of Finland (Kauhala 1996). The disappearance of vole cycles in Lapland has been attributed to the invasion of the generalist mink (Oksanen et al. 2001). Despite these concerns, there have been surprisingly few large scale experimental studies on the possible detrimental effects of mink predation on its prey populations. A long-term mink removal program in the Finnish archipelago revealed negative impacts of mink on the breeding densities of 14 out of 22 bird species, including water fowl, larids, waders and passerines (Nordström et al. 2002; 2003); on the diversity of breeding bird assemblages (Nordström and Korpimäki 2004); and on frog populations (Ahola et al. 2006). Banks et al. (2004) found that mink predation suppressed vole populations on small islands under conditions which otherwise would allow large population increases, suggesting that mink can potentially disrupt meta-population processes in the archipelago. Except for the present study, experimental approaches to investigating the impact of mink on mammalian prey, especially their anti-predatory behaviour, have so far been lacking (Macdonald and Harrington 2003), nor has there been any investigation as to whether mink may induce trophic cascades by reducing the abundance of mammalian herbivores.

This study has therefore focused on the impact of American mink on voles on small islands in the Baltic Sea archipelago. I studied the outcomes of a large-scale, long-term mink removal experiment at the level of the individual (I, II), the population (III, IV) and the ecosystem (V), addressing the following questions:

(1) Are voles able to recognize the threat posed by the alien mink, and do they respond with the appropriate anti-predatory behaviours? More specifically, how does the presence or absence of mink influence the foraging pattern of voles? Do they alter their microhabitat use (I) or their activity timing (II) when mink are present? Are odour cues sufficient to induce the appropriate anti-predatory behaviour, and do voles perceive a co-evolved native predator as more risky than an alien predator (II)?

(2) Does mink play an important role in regulating vole populations on small islands, or is the generally very limited food abundance on these islands more important for the limitation of vole populations (III)? Are vole meta-population processes among islands, especially dispersal and colonisation, influenced by mink presence (IV)?

(3) Does mink induce trophic cascades in the simple ecosystem of small islands? Does mink have an indirect effect on the plant species diversity of the islands via reducing the grazing pressure from voles (V)?

Answering these questions may help us to understand whether and why mink has a detrimental impact on the whole archipelago ecosystem, and may help in finding appropriate management solutions.

2. METHODS

2.1. Study area and species

2.1.1. Study area

The study was conducted on small islands of the Baltic Sea in the outer and outermost zones of the Archipelago National Park in the vicinity of Turku, SW Finland (Fig. 1). The islands are exposed rocky skerries, all smaller than 4 ha in size. Vegetation on these islands is sparse and characterized by grasses (Poaceae, Cyperaceae), dwarf shrubs (bog bilberry *Vaccinium uliginosum* and crowberry *Empetrum nigrum*), heather (*Calluna vulgaris*) and mosses (Bryophyta). The largest islands have solitary trees, while low juniper (*Juniperus communis*) bushes occur on most of the islands.

We conducted experiments in four different areas of the archipelago sea (Fig. 1). Each study area covers 72 – 130 km² and consists of 60 – 77 islands. Two of the study areas had all mink removed, while the other two served as control areas. In removal area R1 around Trunsö near Nauvo (59°49'N, 21°48'E) mink have been consistently removed by gamekeepers since the autumn of 1992; control area C1 around Vänö near Dragsfjärd (59°48'N, 22°11'E), with mink present, has been monitored since spring 1994. Corresponding areas – removal area R2 and control area C2 – were established around Utö near Korppoo (59°47'N, 21°30'E) and Brunskär (60°01'N, 21°23'E) in 1998. In each study area ten islands were defined for the purposes of the present studies as experimental islands. The islands were chosen so to be as similar as possible in size and vegetation cover to support voles. Theoretically it would have been desirable to allocate islands randomly to either mink removal or not, but for practical reasons that was not attainable. Thus this design was the only one that was possible.

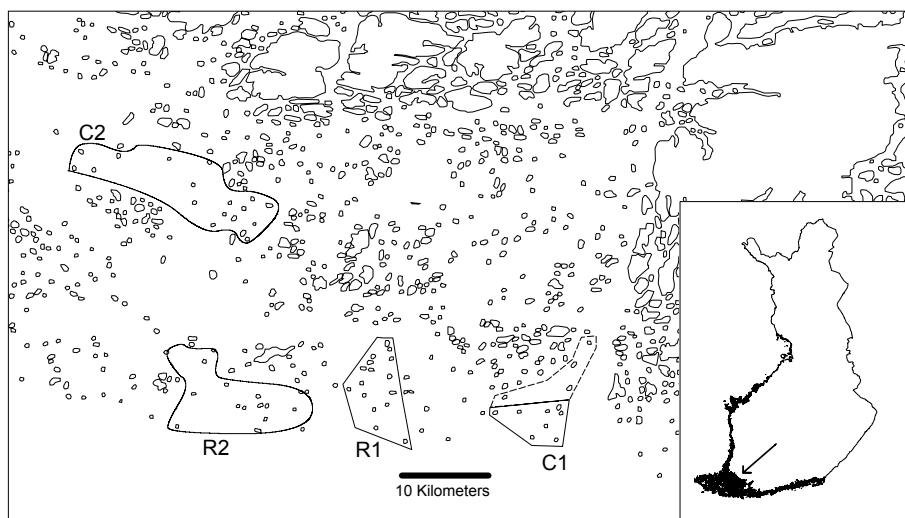


Figure 1. Map showing the study areas in the Archipelago Sea in SW Finland. R1 = removal area 1 (Trunsö), R2 = removal area 2 (Utö), C1 = control area 1 (Vänö), C2 = control area 2 (Brunskär).

2.1.2 American mink

The mink is a North American mustelid species whose native distribution area ranges throughout most of the United States and Canada (Hall 1982). It is a predominantly nocturnal, semi-aquatic species, found in inland wetland habitats and along the coasts (Arnold and Fritzell 1987; 1990). Its diet consists of birds, eggs, mammals, fish, insects, crustaceans and plants (Gilbert and Nancekivell 1982; Jennings et al. 1982).

First introduced into Europe in the early twentieth century, mink has become a successful invader of lakes and along the coastlines of the Baltic Sea. Feral American mink have been present in Finland since the 1950s and have been reported in the Finnish archipelago since the 1970s (Kauhala 1996). The invasion success of mink in Finland was apparently fostered by the absence of natural competitors and enemies.

European mink (*Mustela lutreola*) and American mink are closely related species with similar habitat and food requirements. Since both species have lived in their natural environments on different continents, there has been no need to avoid competition. The lower habitat requirements of American mink, and its ability to thrive well by all kinds of eutrophic waters, while European mink prefers small rivers and brooks, make the larger American species a superior competitor (Westman 1968). Indeed, mink has been blamed for the extinction of European mink in Finland (Maran and Henttonen 1995). In the archipelago, however, European mink has probably never occurred (Westman 1968).

The only natural predator of mink in the archipelago is the white-tailed sea eagle (*Haliaeetus albicilla*), which was absent when mink started to invade the archipelago, but is now returning to breed everywhere in Finnish coastal areas, largely due to effective conservation programmes (Helander et al. 2003; Stjernberg et al. 2005; Salo et al. ms).

2.1.3 Voles

In the archipelago two vole species are found: the field vole (*Microtus agrestis*) and the bank vole (*Myodes glareolus*, earlier *Clethrionomys glareolus*). The field vole is the most common herbivorous small mammal in the archipelago. The bank vole is more patchily distributed and generally more abundant closer to the mainland (Kostian 1970; Ebenhard 1988), but it also occurs in remote areas (Banks et al. 2004). Both species are generalist herbivores subsisting on herbs and grasses, but bank voles are more omnivorous (Henttonen et al. 1977; Myllymäki 1977).

Mink is the main and in fact essentially only mammalian predator of voles in the study area. Other mammalian predators, such as the red fox (*Vulpes vulpes*) and the raccoon dog (*Nyctereutes procyonoides*), are extremely rare on the islands of the outer archipelago, which are too small to sustain permanent populations of these predators (Nordström et al. 2002; 2003). Some predation pressure on voles may be exerted by black adders (*Vipera berus*) and (during the spring and autumn migrations) by short- and long-eared owls (*Asio flammeus* and *A. otus*) and Eurasian kestrels (*Falco*

tinnunculus) (Korpimäki and Norrdahl 1991; Lindell and Forsman 1996; Forsman and Lindell 1997).

On sparsely vegetated small islands, food availability for herbivorous small rodents is severely limited (Pokki 1981; Crone et al. 2001; Banks et al. 2004). Banks et al. (2004) found that vole densities were higher in years with above-average summer rainfall, which increases food availability, than in years with less rainfall. Islands with high summer vole densities showed signs of overgrazing and were also more prone to extinction over the winter, suggesting chronic food limitation.

Vole populations in the archipelago are subject to meta-population dynamics. Island populations are connected by immigration and emigration processes and may experience local extinctions and re-colonisations (Pokki 1981; Crone et al. 2001). In contrast to mainland populations in Fennoscandia (Huitu et al. 2003; Sundell et al. 2004), isolated island populations do not necessarily show synchronisation of population cycles over large areas (Heikkilä et al. 1994; Crone et al. 2001).

2.2. Experimental procedures

2.2.1 Mink removal

For the large-scale removal of mink in the Finnish archipelago, a specific method was developed by Nummelin and Högmander (1998). Mink are tracked by a trained scent hound that is able to quickly find mink on the small islands. After detection, mink usually hide under boulders, rocks or dense junipers. They are chased from these refuges with a leaf-blower, and subsequently killed with a shotgun. Mink removal has been carried out on all the islands in spring and autumn every year. Lethal traps have been used as an additional method. During the first three years, relatively many mink were removed (28–47 / year in both areas); after that the numbers were constantly small (3–12 / year; see Nordström et al. 2003 for exact numbers removed).

2.2.2. Vole trapping

Vole trapping was carried out in a grid of 5 x 5 Ugglan multiple-capture live traps with a trap distance of 10 m, as is typical of vole studies (Norrdahl and Korpimäki 1993; Prévot-Julliard et al. 1999; Klemola et al. 2000). On small islands suitable vegetated habitats are more patchily distributed than on continuous mainland. The traps were therefore not always set at exact 10 x 10 m distances, but were preferably placed on vegetated spots. For a correct assessment of space use by voles (II) we measured inter-trap distances to the nearest 0.10 m with a measuring tape, and recorded microhabitat types within a 1 m radius for each trap (I, II). The traps were baited with standard laboratory mouse pellets or oats. To improve trapping efficiency the traps were pre-baited prior to setting for one day.

Voles were marked individually, sexed and their reproductive status and body mass recorded. The minimum number of individuals known to be alive was used as an index of vole abundance (Krebs 1966; Shaner 2006). When poor weather conditions and logistic constraints forced us to survey vole populations as quickly as possible (III), we

used the number of traps visited (indicated by the loss of bait from these traps) as an index for vole abundance. According to both Lambin et al. (2000) and our own data (III), there is a linear relationship between vole sign indices and vole density estimates derived from live trapping.

In order to obtain more detailed data about activity, home range sizes, survival and microhabitat use of voles, we conducted either intensive trapping, with trap checks every 2 hrs for 24 hrs (II), or radio-tracking of voles (IV). Dispersal was simulated by translocating voles between islands (IV). Voles from both mink islands and mink-free ones were transferred to other islands of both types, to test for the influence of predation risk and experience with mink on the voles' ability to colonise islands.

2.2.3. Simulating predation risk by odour cues

Predation risk was simulated by using either fresh faeces or a liquid extract of faeces. To test whether voles perceive the predation risk posed by a native predator better than that posed by an alien one, laboratory preference tests were conducted in a 1 x 2 x 0.50 m arena using either least weasel (*Mustela nivalis*) or mink faeces (II). To investigate the anti-predatory behaviour of free-ranging voles, we simulated a temporary high predation risk by spraying a liquid extract of mink faeces on the ground inside a trapping grid (II).

2.2.4. Vegetation survey

To detect possible cascading effects of mink removal at the plant trophic level via reducing the grazing pressure of voles (VI), a vegetation survey was conducted on five islands of C1 and nine islands of R1 in 2004, 12 years after the start of mink removal. Ten plots were randomly chosen on each island, and vegetation inside the plots was recorded by a point-intercept method (Levy and Madden 1933; Bråthen and Hagberg 2004) using a 100 x 50 cm plexiglass table with 100 randomly distributed holes. All species hit by a pin passed through the holes were recorded, each species not more than once per hole. The abundance of each species was estimated by the number of holes through which it was hit. The Shannon diversity index and equitability were calculated for each plot as a measure of diversity.

3. RESULTS AND DISCUSSION

The most obvious effect of mink removal was the generally higher vole densities on mink-free islands compared to islands with mink present (III, Fig. 2, see also Banks et al. 2004), which might have been caused by the naïveté of voles against the alien predator and costly anti-predatory behaviours. Differences in vole densities may also have consequences for other trophic levels of the ecosystems. In the following sections, the effects of mink removal on vole individuals and populations are presented in detail.

3.1. Microhabitat use under manipulated mink predation risk

The study showed that voles use different microhabitats on mink-inhabited and mink-free islands. Field voles responded to the presence of mink by a shift from open habitats to juniper bushes, while bank voles avoided juniper in the presence of mink and were significantly more often captured in juniper in removal areas (I). These responses to experimental mink removal indicate that neither rodent species was completely naïve with regard to the predation risk from alien mink. This may be due to their historic coevolution on the mainland with other mustelids, such as weasels and stoats (Cox and Lima 2006). The results for field voles, however, were surprising, as juniper probably provides better shelter against avian predation than against mammalian predators, especially mustelids, which can hunt in small narrow spaces. Furthermore, mink probably prefer juniper as shelter against their predators, such as the sea eagle. The same habitat shift was found in translocated field voles during the colonisation process (IV). In contrast to voles from mink-free islands, voles from mink islands preferred juniper over other habitat types. Field voles apparently lack the appropriate behavioural response, given that they responded with escape tactics against avian rather than mammalian predators. This result is consistent with Banks and Dickman's (2007) level 2 naïveté: recognition of the alien predator but response with an inappropriate tactic.

3.2. Behavioural responses to simulated predation risk

The predator odour treatment had a variable effect on the range of possible risk-sensitive behaviours in voles. In the laboratory, voles avoided the odour cues of the native weasel but not of the alien mink. In the field, voles reduced their activity during typical peak activity times after the mink odour treatment, but no other changes in space use or shifts to safer microhabitats or denser vegetation were apparent (II). It is possible that the response to mink is a context-dependent learned response, which could be induced in the field but not in the laboratory, while the response to weasel is innate. Voles appeared to recognise alien mink as predators from their odour in the wild, most probably because of their close relationship with other small mustelid predators that share a long evolutionary history with voles (Cox and Lima 2006). A reduction in activity, however, is likely to be only a short-term direct response to the immediate mink presence. Prolonged hiding is not sustainable because prey individuals must feed themselves and maintain social activities. The longer-term strategy in

response to repeated mink visitation thus appears to be the use of safer, structurally more complex microhabitats. Taken together, the results of this study (II) and of that on microhabitat use by voles under manipulated mink predation pressure (I) suggest that voles vary their anti-predator behaviour between short- and long-term strategies, and do in fact use mink odour to trigger rapid anti-predator responses.

3.3 Effects of mink predation and food limitation

Study III suggests that vole populations on small islands in the archipelago of the Baltic Sea are mainly bottom-up limited during winter (outside the growing season of food plants), when food availability is low, and by mink predation during summer which slows population growth during the reproductive season of voles. Supplementary food during the winter season had a significant positive effect on vole densities, while the presence or absence of mink had no obvious effect on density changes in vole populations from autumn to next spring. Supplementary feeding during winter also resulted in a higher body mass of voles in spring, and voles from mink-free islands were heavier than those from mink-inhabited ones. The body mass of females was positively influenced by supplementary feeding but unaffected by mink presence, whereas males benefited from both supplementary feeding and mink removal.

Local populations which started to breed with higher densities and better individual body condition were expected to grow faster and show higher densities in summer than populations which were in poorer condition after the winter, due to their probable higher reproductive potential (Ims 1987). In our study system, however, no such long-term effects of supplementary feeding during the previous winter were observed, probably because both natural food abundance and vole densities show high seasonal variability, and during early summer there is more food available than the rather small vole populations in the increase phase can consume (Hambäck and Ekerholm 1997).

Mink removal appeared not to affect density estimates of field voles during the winter and summer immediately after food addition, probably due to small sample sizes and exceptional weather conditions during the study. During an exceptionally mild winter, with the sea freezing over late and for only a short time, the impact of mink on vole survival was probably dampened by the availability of fish as the main prey of mink. Under more adverse weather conditions, the poorer body condition of voles on mink islands and costly changes in their behaviour induced by the mink predation risk (I) may lead to year-round population limitation. Trapping data from 2004-05 and 2007 suggested, that in two out of three summers densities of voles were significantly higher in the absence than in the presence of mink. Thus vole populations on small islands in the archipelago are now under stress year round with limited opportunity to recover. Such prolonged population suppression can add to Allee effects and have important implications for meta-population processes (Martcheva and Bolker 2007).

3.4. Meta-population processes under manipulated mink predation risk

Study IV provided further evidence that alien mink predation may interrupt the meta-population processes which appear to determine the dynamics and distribution of voles in the archipelagos of the Baltic Sea (Pokki 1981), by inhibiting vole colonisation processes. The survival of translocated voles was significantly lower on islands where mink was present compared to control islands. Survival was not improved by former experience with mink. Microhabitat use by “experienced” and “inexperienced” voles revealed the same situation as in study I – voles probably recognised the predation risk associated with the alien predator but responded in the wrong way (level 2 naïveté). While effective anti-predatory behaviour against an alien predator is always critical because of prey naïveté (Cox and Lima 2006; Banks and Dickman 2007), it may be even more limited for dispersers which are not yet familiar with the new habitat. The establishment of colonising field voles in areas with alien mink may therefore fail, leading to the possible extinction of voles in the outer archipelago.

3.5. Mink impact on a lower trophic level

Study V suggests that mink not only limits vole populations (Banks et al. 2004; Banks et al. 2008), but by weakening or eliminating an important source of disturbance – grazing pressure by voles – also reduces plant diversity in the archipelago. Both diversity and equitability of plant communities were higher on islands from which mink had been continuously removed for twelve years. There was also a trend towards changes in plant community structure following mink removal. On the species level, we found the largest number of differences between mink islands and mink free island in grassy patches. The statistically significant species level differences concerned tall herbs and grasses and some palatable species, for which the presence of the mink was a positive factor. The species level results to the opposite direction were not statistically significant. A likely reason for this apparent contradiction is the large number of plant species with good colonizing ability in our study system and the randomness of the dispersal process. When voles create gaps in the vegetation, some of these plants predictably invade, and this is reflected in diversity and evenness indices. However, the identity of invading plants varies between islands and plots, depending on the surrounding vegetation. Therefore, it would require very large materials to obtain statistically significant positive results on the level of individual species.

Our results suggest, for the first time, that an alien predator may induce a trophic cascade on small islands. Since alien mink has also been shown to reduce the diversity of breeding bird assemblages in the outer archipelago (Nordström and Korpimäki 2004), alien predation is not only devastating for native prey populations but can have detrimental effects on the diversity of three trophic levels (piscivorous birds, herbivores and plants) of the ecosystem.

4. CONCLUSIONS

Monitoring all major terrestrial prey of mink and studying their responses to mink removal provides important insights for the conservation of native fauna and the management of feral mink in the Baltic Sea archipelagos and elsewhere. The impact of mink on seabirds and amphibians had been studied before; this thesis has filled in one of the gaps in the study of the impact of mink on the archipelago vertebrate community as a whole. It shows that mink not only has detrimental effects on birds (Nordström et al. 2002; 2003) and amphibians (Ahola et al. 2006), but also affects the individual behaviour of voles (I, II); it may limit vole populations (Banks et al. 2004, III) and disturb their colonisation processes, leading ultimately to the breakdown of vole meta-population processes in the archipelago (IV).

Prey naïveté with regard to a novel predator is often cited as a primary factor in the acute vulnerability of native species (Dickman 1992c; Banks 1998; Short et al. 2002). Voles in the archipelago, however, seem to be able to recognise the predation risk by alien mink, but are unable to respond appropriately. This is what Banks and Dickman (2007) call level 2 naïveté. This can even have more drastic consequences than level 1 naïveté, given that the voles in our studies chose habitats where the danger is even higher than random (I, IV). This result also seems to support the prediction of Cox and Lima (2006) that prey will show similar responses to an alien predator as to a native predator of the same archetype, as well as the common constituents hypothesis (Nolte et al. 1994), according to which odours from closely related predators share common compounds which can be used by prey even when the predators are unfamiliar. Voles should thus be expected to show similar responses to alien mink and native mustelids. Recognition of olfactory cues in rodents can occur in two places in the olfactory bulb, one representing innate recognition and the other an process through prior experience (Kobayakawa et al. 2007). The innate avoidance of predators may last a long time; learned anti-predatory behaviour, in contrast, is rapidly lost in the absence of predators, but is also quickly regained with repeated exposure to the predator (Blumstein 2002). Olfactory recognition of native mustelids as the least weasel seems to be innate; voles from the archipelago seem to recognise the least weasel as a threat (II), even though they have been separated from mustelid predators since the land uplift following the ice age, which formed the archipelago, about 10 000 years ago. Recognition of alien mink odours, on the other hand, seems to be a context-dependent learned behaviour, which works in the field but not in the laboratory (II).

Yet this lack of naïveté does not prevent mink from impacting on vole populations and threatening their long-term persistence in the area. Recognition of an alien predator will not necessarily provide protection if the native prey responds with tactics which fail to work against the different hunting modes of alien predators.

Voles are certainly not of the highest conservation interest. However, they play an important role in the ecosystem. Reduced grazing pressure also reduced plant diversity in the archipelago (V), and if vole populations decline or become locally extinct this will probably decrease the abundance of their native predators (black adders, birds of

prey), which in turn will have far-reaching consequences for the whole archipelago ecosystem.

American mink should therefore be carefully managed to avoid further damage to the archipelago ecosystem. Management should include prevention of further escapes and rapid response after releases, continuing local control or eradication, and promotion of the natural recovery of native mink predators and competitors (Bonesi and Palazon 2007). The ongoing increase of the white-tailed sea eagle populations in the archipelago area may be effective in mitigating the adverse effects of alien mink (Salo et al. ms).

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