

Impacts of alien mink predation on island vertebrate communities of the Baltic Sea Archipelago: review of a long-term experimental study

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Feral American mink (*Mustela vison*) are emerging as one of the biggest threats to biodiversity in northern Europe. Here we summarize responses of migratory seabirds, island small mammals and amphibians to 15 years of large-scale, experimental mink removal in the outer Finnish archipelago. Mink control led to increases in breeding populations of 14 of 22 species of seabirds, which were generally of smaller body size and later breeders as compared with those species which showed no responses. Mink also suppressed the natural summer increases of bank vole (*Clethrionomys glareolus*) and field vole (*Microtus agrestis*) populations but only during years of good rainfall. Impacts on common frogs (*Rana temporaria*) took seven breeding seasons to appear probably because of delayed maturation of frogs; the less palatable common toads (*Bufo bufo*) seemed unaffected. It appears then that the disruptive effects of mink impacts may cover the entire island vertebrate community with cascading consequences to the whole archipelago ecosystem. Ongoing research is focused on the effects of the native apex predator, the white-tailed sea eagle (*Haliaeetus albicilla*), whose return may suppress the detrimental effects of mink.

Introduction

Alien terrestrial predators are considered the worst of the world's invasive species (Gurevitch and Padilla 2004). Predation by introduced predators has caused some of the most rapid and severe changes in native bird and mammal populations; the devastation wrought by Brown tree snakes in Guam (Savidge 1987, Fritts and Rodda

1998), rats in Polynesia (Blackburn *et al.* 2004), and foxes and feral cats in Australia (Dickman 1996) are now infamous examples of the potential for alien impacts on biodiversity. Introduced predators are considered responsible for at least 40% of the 127 birds extinction events that have taken since 1600 AD (Newton 1998), and they are currently responsible for endangering 40% of the threatened island bird species (King 1985

in Courchamp *et al.* 1999, *see also* Birdlife International 2000). And there are many more species that have become locally extinct, are threatened or have declined where predation by alien predators remains a key threatening process.

The effects of introduced predators seem to have been especially pronounced in simple systems, such as oceanic islands and archipelagos, where there have traditionally been few native ground-living mammalian predators if any. Native prey may be at a distinct disadvantage to alien predators which may not be recognised as dangerous (e.g. Banks 1998) or may induce the wrong anti-predator behaviours (Banks and Dickman 2007). Cox and Lima (2006) used the term “predator archetype” to describe the relative similarity between the alien predator and native predators. They predicted that impacts of aliens of a distinctly different predator archetype to the native fauna would be greatest. In a recent world-wide review of predator removal experiments, Salo *et al.* (2007) found some support for this concept; alien predator impacts were worst in insular ecosystems but only if Australia was considered an island given its unique evolutionary history. They also found that there had been relatively few studies of alien predators outside such insular ecosystems where the predator was typically a distinctly novel archetype.

In Europe, the American mink (*Mustela vison*) (hereafter mink) has been suspected of having a notable negative impact on some of its prey species. The mink is a semi-aquatic North American species, which escaped to North European environments over 80 years ago from fur farms (Dunstone 1993). Its recent distribution covers the semi-aquatic ecosystems (wetlands, archipelagos, river catchments, etc.) of northern and eastern Europe (Dunstone 1993), including outer archipelagos and Lapland in the north (Kauhala 1996) and more recently the British Isles (Macdonald and Harrington 2003) and southern Europe (Delibes *et al.* 2004). Like many successful invaders, mink are generalist predators, preying upon birds, fish, frogs and small mammals depending upon local availability. American mink in Europe do not necessarily represent a novel predator archetype because there is a high diversity of other mustelid predators across the continent (King 1989), including the native

European mink (*Mustela lutreola*) which in some areas is thought to have been replaced by the North American invader and is now threatened (Macdonald and Harrington 2003).

But across the mink’s European distribution there has still been concern about the impacts of mink predation on each of its major prey types. In Britain, mink have been linked to the widespread decline of the water vole (Macdonald and Harrington 2003), and the wave of water vole decline in Scotland has been correlated to the spread of the mink (Aars *et al.* 2001). There is concern over mink impacts on ground nesting birds in Britain (Ferrerias and Macdonald 1999), Scotland (Craik 1997, Moore *et al.* 2003), Poland (Bartoszewicz and Zalewski 2003), and mainland Finland (Kauhala 2004). In Spain there is also emerging concern over mink impact on intertidal fauna (Delibes *et al.* 2004). Despite these concerns, there have been surprisingly few experimental studies carried out on the possible detrimental effects of feral mink predation on its prey populations in Europe. This contrasts with the large number of experimental studies dealing with the impacts of native small and medium-sized mammalian predators on their prey populations (Salo *et al.* 2007).

Experimental study of the impact of vertebrate predators on landscape scale has turned out to be very challenging, except perhaps for on isolated islands (but *see* Pech *et al.* 1992, Krebs *et al.* 1995, Banks *et al.* 1998, Banks 1999, 2000, Korpimäki and Norrdahl 1998, Korpimäki *et al.* 2002, 2005). There are at least three important reasons which may cause these challenges. Firstly, it may be extremely difficult to remove all individuals of a predator species; and dispersing individuals from the surroundings may soon restore the predator population (Byrom 2002, Korpimäki *et al.* 2002). Therefore, continuous and year-round removal is essential or the predator reduction period will remain short. Secondly, where only one predator species is removed, intra-guild predation will relax and remaining predators may increase their predation rate to dilute the effect of removal (Norrdahl and Korpimäki 1995, Korpimäki and Norrdahl 1998). And finally, in the absence of intra-specific competition for resources any remaining predators (or the re-colonising individuals) may

increase their reproduction effort and/or survival, and may thereby in the short term even increase their predation rate compared to pre-removal conditions (Boyce *et al.* 1999). For the prey community, reduced predation pressure may lead to increasing inter-specific competition and a stronger competitor may start to dominate the system (Paine 1966, Henke and Bryant 1999). Islands and insular systems are well-suited to large-scale predator removal, because of the generally fewer predator species and slower recolonisation rates than on the mainland. Thus, more substantial effects of predator removal on prey populations can be expected and have been reported from several studies of insular ecosystems (e.g. Côté and Sutherland 1997, Macdonald *et al.* 1999).

In this paper, we summarise the outcomes of a 15-year mink-removal experiment conducted in the outer archipelago of the Baltic Sea and report on the long-term responses of the major prey of mink; birds, small mammals and amphibians. In doing so we address the following management questions:

1. What are the effects of mink predation on the spatial distribution of the breeding bird community occupying a naturally fragmented archipelago habitat?
2. What are the effects of mink removal on populations of different breeding birds in the outer archipelago of the Baltic Sea, and which characteristics make a species more vulnerable to mink predation risk than others?
3. Is predation by mink affecting the dynamics of herbivore mammals (voles) and amphibians in the naturally fragmented archipelago habitat?
4. Are prey (voles) naïve to the predation risk posed by alien American mink?

Methods

Detailed information about the study area, mink control and survey methodology for birds, voles and amphibians are given in Nordström *et al.* (2002, 2003), Banks *et al.* (2004) and Ahola *et al.* (2006). Below is a summary of the key methodologies.

Study area

The study was conducted on small islands of the Archipelago Sea, southern Gulf of Bothnia SW Finland, in two phases. From 1993 to 2001, bird and frog surveys were conducted in a mink removal area near Nauvo (R1: 60 islands spanning 72 km²) and in a control area in Dragsfjärd (C1: 35 islands in 37 km²). In the second phase, the study was extended to include an additional removal and control areas near Korppoo (R2: 62 islands in 125 km², C2: 64 islands in 130 km²) and additional surveys for birds, small mammal and frogs were conducted. Islands in all areas comprised small rocky skerries (approx. 75% < 2 ha), of which the smallest have only sparse vegetation comprising tiny patches of grass, while the large island have extensive patches of juniper. Trees (Scots pine and mountain ash) were scarce and solitary; ponds were common. Island size and relative isolation varied across the study areas and were included as covariates in all analyses using indices of isolation based on Hanski *et al.* (1994).

Study species

American mink is a predominantly nocturnal medium-sized mammalian predator that is attracted to all kinds of waters (streams, lakes, creeks, sea) and archipelagos. First introduced to Europe in the early 20th century, it has been a successful invader of lakes and coastlines of the Baltic Sea (Long 2003). This success is mainly due to its swimming capability, dietary flexibility (mainly fish, small mammals, birds, amphibians, crustaceans) and the absence of natural competitors and enemies. Wild American mink have been present in Finnish environments since the 1950s and have been reported in the Finnish Archipelago since the 1970s (Kauhala 1996). European mink have been absent in the archipelago (Westman 1968). Analysis of 2922 scats of alien mink in the study area (1992–1997) showed that their diet (% occurrence in scats) consisted of 42% fish, 32% birds (mainly common eider *Somateria mollissima*), 13% mammals (mainly field vole *Microtis agrestis*), 11% insects, molluscs and plant matter, and 2% common frogs (*Rana term-*

poraria) (N. Laanetu and J. Nummelin unpubl. data; *see also* Niemimaa & Pokki 1990). More recent data (2004–2005) indicated that the corresponding proportions were 33% for fish, 28% for birds, 15% for mammals, 8% for crustaceans, 6% for insects and 10% for other prey groups (M. Toivola and P. Salo unpubl. data).

For this experimental study, a specific mink removal method was developed by Nummelin and Högmander (1998). Mink were tracked by a trained scent hound, which is able to rapidly find mink on small islands. After detection, mink usually hide under dense junipers, boulders or rocks. To chase mink from these refuges, various methods — including water and smoke — were first tested. The use of a leaf-blower, however, was found to be most suitable to drive mink from its hiding place. A shotgun was then used to kill the mink. Lethal traps were used as an additional method, both in the removal areas and on surrounding islands which acted as a buffer zone. Mink removal was carried out on all islands in autumn and spring each year and proved very effective. The number of mink removed in R1 declined from 63 individuals in 1992/1993 to 3 in 1998/1999 and to 0 in 2000; in R2, 50 mink were removed in 1998/1999 and few signs of mink were detected thereafter. We collected sightings and various signs of mink: scats, killed prey items and tracks from all areas in order to estimate which islands had been visited by mink. This method, however, does not enable to estimate the mink population, since it does not reveal the number of individuals, and at least some signs are probably not discovered.

Archipelago birds

Birds in the outer archipelago of the Archipelago Sea are mostly migratory. They breed on the ground and many species are colonial or colony-associates. Compared with many other archipelagos, the Finnish Archipelago Sea constitutes a small-scaled mosaic of thousands of various-sized islands. Inter-island distances are small, and therefore, the isolation of islands does not reduce the dispersal of archipelago birds (von Numers 1995). Birds were censused on all islands in each study area, three times during

the breeding season following survey methods for archipelago birds outlined in Hildén (1964) and Hildén *et al.* (1991) which involves a combination of nest counts and counts of broods or pairs. Breeding was confirmed by nests found or parental behaviour.

Voles

In the archipelago of SW Finland two species of voles are found: the field vole (*Microtus agrestis*) is widespread and found even on the outermost islands, while the bank vole (*Clethrionomys glareolus*), is more patchily distributed and generally more abundant closer to the mainland (Kostian 1970, Ebenhard 1988), although it too is found in the outer archipelago. Both species are generalist herbivores subsisting on herbs and grasses but bank voles are more omnivorous (Henttonen *et al.* 1977, Myllymäki 1977).

Vole populations in the archipelago were considered true metapopulations, because islands are connected by immigration and extinctions and re-colonisation events are common (Pokki 1981, Crone *et al.* 2001). Isolated island rodent populations may not necessarily be synchronised over large areas (Heikkilä *et al.* 1994, Crone *et al.* 2001), as is typical for mainland populations (Huitu *et al.* 2003, Sundell *et al.* 2004). Voies were surveyed on 10 islands by live-trapping over 3 nights in each study area in autumn of 1998, 1999 and 2000. Only islands considered suitable for voles (> 1 ha and containing suitable hay vegetation and refugia) were sampled. In 1999, we additionally studied habitat use of voles under manipulated mink predation risk by relating trap success to microhabitat characteristics around trap locations. Microhabitat characteristics were classified into four types reflecting risks of mink predation and suitability for foraging: grassy patches, juniper bushes, berries and open habitats and then compared with microhabitat availability (*see Fey et al.* 2006).

Amphibians

Common frogs and common toads (*Bufo bufo*) inhabit the freshwater ponds on the islands. The

number of ponds varied among years because of climatic factors, thus we counted the minimum number of suitable ponds on each island. We excluded islands that lacked freshwater ponds, as well as small (smaller than 1 ha) isolated islands (with ponds but without appreciable vegetation) further than 1 km from nearest vegetated, larger island. Annual spring surveys of frogs and toads were performed from the last week of April until the third week of May and began in the springs of 1993 (R1) and 1998 (R2, C1, C2). Common frogs lay one egg batch per female at the end of April, while common toad females lay their eggs in distinctive strings ca. one week later. The number of egg batches and egg strings can therefore be directly used to index the number of reproducing adult females in a population (Laurila 1998).

Results and discussion

Mink in the archipelago

Island size and isolation were related to the occurrence of mink; more signs were found on larger and less isolated islands in one control area (Nordström *et al.* 2004). However, mink were sometimes found on highly isolated islands as well, indicating that all islands in the study areas are accessible to mink but that they are most likely to be found in less fragmented parts of the archipelago. Given that the breeding season of birds is short, mink may not risk the long swim to isolated and small islands. Large, less isolated islands may also have more habitats for voles and fish, which are the main food for mink outside the breeding season of birds.

Bird distribution, island characteristics and mink removal

Long-term exposure to mink predation (together with predation risk, *see* Nordström *et al.* 2004) appears to have modified the distribution of the bird community in the outer archipelago. In control areas with mink, islands with the highest diversity and abundance of birds were the most isolated ones whereas in mink removal areas the bird community was equally diverse

and abundant on all types of islands, regardless of isolation (Nordström and Korpimäki 2004). The diversity and abundance of birds was also positively related to island size, and tended to be higher on larger islands in mink removal areas than in control areas, but lack of variation in island size prevented clear resolution of this issue. Predation pressure by mink appeared to affect nest site selection as birds in control areas mostly bred on isolated islands where the probability for mink occurrence was low. It is possible that heavy predation caused seabirds to abandon their breeding colonies (Burger 1982, Whittam and Leonard 1999) or that birds may have actively selected such nest sites where predation risk was lower (*see* also Andersson 1992, Martin 1993, Kilpi 1995). It is also possible that some bird populations in less fragmented parts of the control areas may have been reduced through long-term predation by mink.

One explanation of these overall patterns in bird distributions is that mink predation first induces breeding failures of birds on less isolated islands, which is followed by an abandonment of the breeding site. Failed breeders may then select their new breeding site through conspecific or hetero-specific attraction (*see* below) on islands where breeding success is high and predation risk is low. This will result in higher diversity and abundance of bird communities on isolated islands, but also in mink removal areas. Archipelago birds may thus have responded to the risk induced by mink by starting to breed on the most isolated islands in areas colonised by mink.

Bird population changes and characteristics

One of the most valuable findings of the mink removal experiment for conservation purposes and the protection of biodiversity is that mink removal led to marked and rapid increases in the breeding densities of many bird species (Nordström *et al.* 2002, 2003) and the increases in the numbers of species breeding per island (Fig. 1). Of 22 species studied, populations of 14 species increased after mink removal, while seven species were unaffected and one appeared to decline (Table 1).

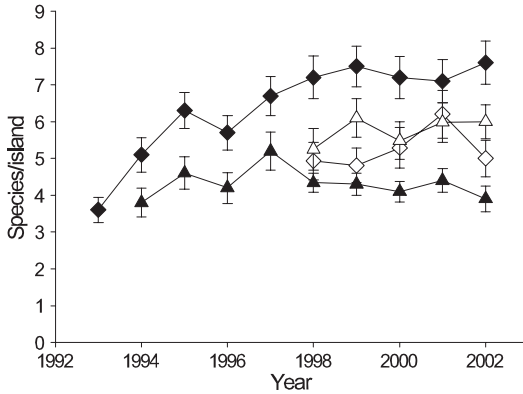


Fig. 1. The response of mink removal on the diversity of breeding populations (number of species per island with standard errors). ◆ = long-term removal area, ◇ = short-term removal area, ▲ = long-term control area, and △ = short-term control area (figure modified from Korpimäki and Nordström 2004).

Two characteristics of birds appeared to be associated with an increased vulnerability to mink predation: body size, timing of late breeding; association with larid colonies may also be important for some species (Table 1). The species that showed a positive response to mink removal were late breeders (SAS pure GENMOD, logistic regression: $\chi^2 = 8.95$, d.f. = 1, $P = 0.003$) and small sized within their order (waterfowl, Anseriformes, or waders and larids, Charadriiformes included, alcids and passerines not included) ($\chi^2 = 6.60$, d.f. = 2, $P = 0.04$). Association with small larid colonies could not be included in this model due to small sample size. Adult birds of small and medium sizes may be a more suitable prey for mink than larger species, which may also be more successful in the protection of their nest and young. Timing of breeding may be of importance, since minks are born in late April–early May, and their food requirements increase in early summer as they also become more mobile (Dunstone 1993). Seabird colonies may be effective to protect themselves against diurnal avian predators, but they cannot defend against nocturnal predators (Hunter and Morris 1976). In fact, colonies may be easy to find and thus attract predators (Clode 1993).

The rapid population increases for some species following mink removal was not solely a consequence of improved recruitment derived from the breeding of local populations. More

breeding birds were detected in just a few years of mink removal even though some of the species which responded take several years to reach breeding age; the common gull, arctic tern and the arctic skua start to breed in their 4th–5th calendar-year, the velvet scoter in its 3rd–4th and the turnstone from its 3rd calendar-year onwards (Cramp and Simmons 1977, Hario 1986, Hildén and Hario 1993). There are at least three factors which might have led to the rapid population increases, including predator-avoidance mechanisms (Norrdahl and Korpimäki 1998), attraction to predator-free areas for breeding (Duebbert and Lokemoen 1980), and conspecific-attraction mechanisms (Stamps 1988, Danchin and Wagner 1997). Theories on conspecific attraction propose that immature individuals and failed breeders may use the presence and colony size of conspecifics as cues in their future breeding habitat selection (the conspecific-attraction hypothesis; Stamps 1988), or that non-breeders prospect in several breeding habitats and use the current reproductive success as a cue to select their next year breeding site (the conspecific-reproductive-success hypothesis; Danchin and Wagner 1997, see also Danchin *et al.* 1998, Fredriksen and Bregnballe 2001). Furthermore, birds may use the presence of heterospecifics as a cue that an area has low predation risk or a favourable food supply (the hetero-specific attraction hypotheses; Mönkkönen *et al.* 1990, see also Elmberg *et al.* 1997, Forsman *et al.* 1998). Therefore, mink removal areas may attract both colonial small larids, due to e.g. successful reproduction, and consequently also those species that are associated with breeding colonies.

Vole metapopulation dynamics and mink predation

Mink had a strong effect on vole populations, but not in all years (Banks *et al.* 2004). In 1998, when above average rain fell during the summer breeding season, bank vole densities were 6.2 times higher, and field voles were 5.5 times higher in removal areas as compared with those in control areas. But these differences disappeared in 1999 and 2000 when summer rainfall was below average (Banks *et al.* 2004). As rain-

Table 1. Summary of effects of mink removal on each bird species' breeding population, and its body size, mean egg-laying period, association with larid colonies in the outer archipelago and comments.

Species	Mink removal effect	Body weight (g) ^{1,2,3,4}	Egg-laying period ^{1,4,5}	Association with larid colonies ^{5,6}	Comments to colony association
Mute swan (<i>Cygnus olor</i>)	none	10000	1–5 May	positive (small larids)	habitat preference? (egg-laying differs)
Grey-lag goose (<i>Anser anser</i>)	none	3500	26–30 Apr	none	
Shelduck (<i>Tadorna tadorna</i>)	positive	1200	11–15 May	none	
Mallard (<i>Anas platyrhynchos</i>)	positive trend	1100	6–10 May	none	slightly positive (small larids)
Tufted duck (<i>Aythya fuligula</i>)	positive	680	31 May–4 Jun	positive (small larids)	
Common eider (<i>Somateria mollissima</i>)	none	1700	26–30 Apr	positive (large larids)	
Velvet scoter (<i>Melanitta fusca</i>)	positive	1600	10–14 Jun	positive (small larids)	weak (small larids)
Goosander (<i>Mergus merganser</i>)	none	1300	26–30 Apr	none	
Oystercatcher (<i>Haematopus ostralegus</i>)	none	480	11–15 May	positive (small larids)	
Ringed plover (<i>Charadrius hiaticula</i>)	positive	58	11–15 May	positive (small larids)	
Redshank (<i>Tringa totanus</i>)	positive trend	107	16–20 May	positive (small larids)	
Turnstone (<i>Arenaria interpres</i>)	positive trend	104	31 May–4 Jun	positive (small larids)	
Arctic skua (<i>Stercorarius parasiticus</i>)	positive	480	21–25 May	none	kleptoparasites on small larids
Common gull (<i>Larus canus</i>)	positive trend	360	21–25 May	constitute colonies	number of colonies increased
Gr. black-backed gull (<i>L. marinus</i>)	none	1400	1–5 May	positive (herring gull)	
Arctic tern (<i>Sterna paradisaea</i>)	positive	120	21–25 May	constitute colonies	number of colonies increased
Flazorbill (<i>Alca torda</i>)	positive; recolonized	710	31 May–4 Jun	constitute colonies	breeds in species-specific colonies
Black guillemot (<i>Cepphus grylle</i>)	positive; recolonized	430	31 May–4 Jun	none	breeds in species-specific colonies
Meadow pipit (<i>Anthus pratensis</i>)	negative	18	16–20 May	none	
Rock pipit (<i>A. petrosus</i>)	positive	25	21–25 May	none	
White wagtail (<i>Motacilla alba</i>)	none	20	11–15 May	none	
Northern wheatear (<i>Oenanthe oenanthe</i>)	positive	23	16–20 May	none	

Sources: ¹ von Haartman et al. (1963–1972), ² Hario (1986), ³ Cramp and Simmons (1977), ⁴ M. Nordström (unpubl. data), ⁵ Hildén and Hario (1993), ⁶ von Numers (1995).

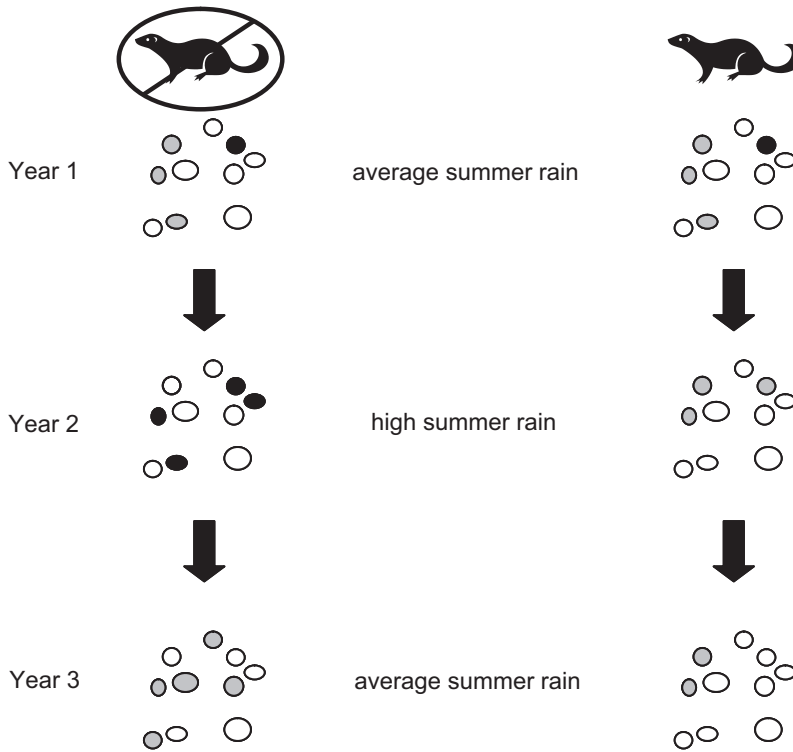


Fig. 2. Conceptual model of the impacts of feral mink predation on vole metapopulation dynamics in island ecosystems. Empty circles = vacant islands, grey circles = island with low vole densities and black circles = islands with high vole densities. Without mink, some islands go extinction and others are colonised by dispersal under average conditions, but high summer rains leads to rapid increases in vole numbers on all islands and enhanced dispersal and colonisation in subsequent years. With mink predation extinctions still occur but post-rain irruptions do not, leading to reduced dispersal and colonisation and a gradual erosion of vole distribution.

fall is directly related to vegetation productivity on such small islands, it seems that even without mink, vole populations can increase only when conditions allow. Island isolation was negatively related to occupancy for both bank voles and field voles, and bank voles were entirely absent from R2, the most isolated area. Previous density also affected subsequent occupancy, with a high proportion of extinction on islands that had very high densities in the preceding autumn.

We propose that processes affecting vole distribution (isolation) and populations (mink) may interact to affect the metapopulation dynamic (Fig. 2). Without mink, vole populations boom during good years only to bust the following winter when islands run out of food. And the provision of supplementary food leads to higher populations sizes in the following spring, suggesting winter food limitation (Fey *et al.* unpubl. data). Such chronic food stress and social pressure resulting from high densities would be a major driver of dispersal, and we observed most dispersal during high density years. This dispersal leads to re-colonisation of small islands which are naturally prone to extinction and is

vital for maintaining the regional metapopulation (Crone *et al.* 2001). Alien mink, however, appear to suppress population booms which can remove the motivation to disperse. In this scenario, we predict that alien predators can lead to the breakdown of metapopulation dynamics and ultimately lead to local extinction of voles (Fig. 2).

Recovery of amphibian populations

During the last years of the long-term removal experiment (1998–2001), there were more reproducing common frog females per island in the long-term removal area (R1) than in the short-term removal area (R2) and the two control areas (C1, C2) (Ahola *et al.* 2006). Frogs in the short-term removal area (R2) were significantly more abundant only in one control area (C1). Numbers of frogs in R1 increased on average by 46% per year for the first six years (1993–1998), until the seventh spring (1999) when their numbers increased 462% from the preceding year, and more than doubled (119% increase)

from the seventh to ninth spring (1999–2001). These increases, after that many years of predator removal, indicated an involvement of some internal factors in population limitation. We suggest that common frogs have a delayed maturation in the harsh conditions of the outermost archipelago and the largest increase, which was observed in the seventh spring, occurred due to the maturation of the first common frog generation born after mink removal. This showed that only a long-term experiment could reveal the whole extent of the removal effect.

Common toads did not benefit from the mink removal as clearly as the common frogs. Toads were overall much less abundant than frogs. Fewer numbers were found in the long-term removal area (R1) than in the two control areas (C1, C2). This might reflect an advantage of toads due to selective predation by mink in the control areas, as toads are protected against mink predation by their unpalatable skin. However, the difference between areas can also be a result of the vicinity of larger islands outside of each area, as those are the primary habitats for toads in the archipelago (Ahola *et al.* 2006).

Behavioural responses of voles to mink presence

Voles responded to the presence of mink by a shift in microhabitat use; field voles shifted from open grassy habitats to juniper bushes whereas bank voles avoided juniper in the presence of mink and were significantly more often captured in juniper in removal areas (Fey *et al.* 2006). These responses to experimental mink removal indicate that neither rodent species was completely naïve to predation risk from alien American mink. This may be due to historic co-evolution on the mainland with other mustelids such as weasels and stoats (Cox and Lima 2006). But the results for field voles 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 prefers juniper as shelter against its predators, such as the sea eagle. It seems that field voles may lack the appropriate behavioural

response given that they responded with escape tactics against avian rather than mammalian predators. This result fits in with Banks and Dickman's (2007) level 2 naiveté; recognition of alien but response with an inappropriate tactic. Nevertheless, despite predator recognition and anti-predator behaviours by voles, alien mink still significantly suppress vole populations of both species (Banks *et al.* 2004).

General implications for alien predator removal campaigns

By monitoring all major terrestrial prey and tracking their long-term responses to mink removal, our study represents one of the most comprehensive experimental examinations of the impacts of alien predators. The summary presented here on the response of the whole vertebrate community to mink removal provides several important insights for the conservation management of alien predators.

Firstly, almost all prey species studied showed negative impact of mink predation, including some prey which comprised only a small part of the mink diet. Such widespread responses across the entire vertebrate community support the concern about mink as an alien invader in Europe (Macdonald and Harrington 2003). Nevertheless, the fact that not all prey species responded to mink removal suggests that for some species, alien predation may be a compensatory source of mortality rather than an additive source, even though mink-like predators are rare or absent from the archipelago. Some species simply did not increase, even with evidence of low levels of predation whereas other species (toads) appeared to benefit from some pre-adaptation to predation risk from mink. These results point to the difficulty in *a priori* predictions of alien predator impact.

Secondly, the impacts of alien predation may take many years to appear, depending on the life-history of the prey and the environment. While the benefits of mink control were immediate for some species such as voles, increases in frogs took 7 years corresponding to the time for sexual maturity in the species. Thus even though some species may not respond, experiments need to

persist long enough to give prey a chance to show a response.

Thirdly, alien impacts may interact with environmental conditions such as weather; vole populations showed a dramatic response to mink removal in the first year of study, but only because rainfall conditions were sufficient to enable population increase. When too little rain fell, populations could not increase despite the absence of mink. Thus interpretations of removal experiments must consider the potential role of bottom up, exogenous forces on the nature of prey responses.

Fourthly, alien predation can clearly alter distributions of their prey. Most previous work on alien predators has largely focussed on population level responses. Yet long-term mink removal led to increases in the large-scale distribution of frogs, and some birds. For some species, this was probably a by-product of population level increases. However for voles we predict that future changes to distribution arise because the natural vole metapopulation processes are being threatened by the stabilizing impact of mink predation that dampens boom-bust dynamics. Indeed the stabilizing impact of alien predation could threaten the long term persistence of any fragmented populations which relies upon inter-population dispersal.

Finally, the role of prey naiveté in alien impact is not straightforward. Voles appeared to recognise alien mink as a risk and responded with anti-predator behaviours, which for bank voles at least were consistent with their responses to predation risk from other mustelid native predators (Jedrzejewski *et al.* 1993). Yet this lack of naiveté did not prevent mink from impacting upon vole populations and threatening their long-term persistence in the area. Thus a lack of naiveté will not necessarily afford protection from alien predators where such predation functions as an additive source of mortality.

Future prospects

Top avian predators, for example, white-tailed sea eagles (*Haliaeetus albicilla*), golden eagles (*Aquila chrysaetos*) and eagle owls (*Bubo bubo*),

disappeared from much of their European range > 50 years ago. For example, the white-tailed sea eagle (hereafter sea eagle) population in Finland suffered a drastic decline in the 1960s and 1970s, but has rapidly increased due to efficient conservation programmes: there were 75 occupied sea eagle breeding territories in Finland in 1990 whereas the corresponding number was 249 in 2004 (Stjernberg *et al.* 2005). The probable consequences of the drastic decrease of sea eagles have been the marked relaxation of fear factor on small to medium-sized carnivores and birds of prey, which may have induced a mesopredator release (Courchamp *et al.* 1999) and biodiversity loss (Sergio *et al.* 2005). Therefore, the invasion of mink to outer archipelagos of the Baltic Sea may have been facilitated by the virtual absence of sea eagles at the same time. Alien carnivores (American mink and raccoon dog), native carnivores (foxes, martens and weasels) and smaller birds of prey entail 1%–2% each of the diets of breeding sea eagles, golden eagles and eagle owls in northern Europe (Korpimäki and Nordström 2004, Valkama *et al.* 2005). While that percentage seems low, the densities of predators are usually an order of magnitude lower than the densities of their herbivore prey. In addition, during autumn and winter, the presence of young inexperienced individuals will likely lead to higher predation risk of these species by top avian predators. Therefore, these apex predators may act as an important mortality and fear factor for small to medium-sized carnivores and birds of prey. For instance, as a consequence of a human-induced invasion of golden eagles on the Californian Channel Islands, USA, predation by golden eagles led to a drastic decrease of an endemic small fox species (Roemer *et al.* 2002, *see also* Sunde 2005).

The ongoing rapid return of sea eagles to the archipelagos of the Baltic Sea and mainland of Fennoscandia provides a unique opportunity to examine, whether this native top predator, occupying its territories throughout the year could provide ecosystem services. We hypothesise that the re-establishment of top avian predator territories will create a landscape of fear for smaller native and alien carnivore species that could suppress their recent increases and in turn could

benefit lower trophic levels. We suggest that by the suppressing more abundant medium-sized to small carnivore populations, sea eagles could probably more than compensate for the losses of small game animals (e.g. waterfowl) caused by their direct predation (e.g. *see* Milonoff 1994).

Our ongoing research is focused on the effects of the return of sea eagles which can both kill and intimidate mink. Our hypothesis is that the return of sea eagles will at least partly suppress the detrimental effects of mink on the archipelago ecosystem. Our preliminary results show that radio-collared reproducing mink females avoid swimming trips between islands in areas of high sea eagle-risk but not so much in areas of lower sea eagle-risk (P. Salo and E. Korpimäki unpubl. data). This provides the first support of our hypothesis that when swimming mink are particularly vulnerable to eagle predation, and therefore, that intimidation by sea eagles may reduce food intake and reproductive rate, and thus limit population size of mink. Therefore, at least four predictions can be made on the basis of our detailed knowledge of archipelago ecosystems. Increasing densities of sea eagles may:

1. Suppress detrimental impacts of mink on voles and thus relax the cascade to plant trophic level. This should increase the grazing impacts of voles on vegetation.
2. Decrease the destructive impacts of mink on common frogs, which may cascade to the insect food of frogs and thus relax the effects of insects to lower trophic levels.
3. Decrease the harmful impacts of mink on seabirds, which may cascade, for example, to insect, fish, gastropod and crustacean foods of seabirds and thus relax the effects of these animal groups to lower trophic levels.
4. Decrease the detrimental impacts of mink on predatory fish including perch (*Perca fluviatilis*), which may in turn strengthen the cascades to lower trophic levels, including herbivorous fish and the isopod (*Idotea baltica*), the main grazer of algae belt including brown alga. Brown alga belt in the Baltic Sea has decreased because of eutrophication (Hemmi and Jormalainen 2002).

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