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Variable responses of waterfowl breeding populations to long-term removal of introduced American mink

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It is suspected that feral American mink, an introduced predator in Europe, have seriously affected local densities of birds breeding in archipelagos and coastal areas. We studied the effects of mink removal on breeding densities of waterfowl in two manipulation and two control areas in the outer archipelago of SW Finland, Baltic Sea. The study was conducted in two phases: during 1992–2001 a total of 98 mink was removed from 60 islands and islets (total area 72 km^2) whereas on 37 islands and islets (35 km^2) mink was not removed. Additional mink removal and control areas were established during 1998–2001 to replicate the experiment. The breeding densities of the shelduck, tufted duck and the velvet scoter increased as a response to mink removal, while in the control areas their populations remained unchanged. The breeding densities of mallards increased during the first 7 yr of mink removal, but a steep decrease in the last study year resulted in a statistically non-significant overall increase. The species with low breeding densities (the gadwall, northern shoveler, pintail and the red-breasted merganser) increased as well. In contrast, the populations of large waterfowl species, the mute swan, greylag goose, common eider and the goosander, did not show obvious increases in breeding densities after mink removal. We conclude that feral mink may locally limit the breeding densities of some smaller waterfowl species and thus reduce the diversity of the waterfowl community in the outer archipelago.

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Predation is considered to be one of the most important factors limiting population densities of vertebrate animals, but other factors may also limit vertebrate populations, including food supply, availability of nest and refuge sites, conditions in wintering areas, diseases, parasites and competition (Begon et al. 1996, Newton 1998). Introduced predators have caused population declines or even local extinction in many native organisms, especially in bird populations on oceanic islands where the native species have not adapted to ground-living predators (Groombridge 1992, Newton 1998). The removal of vertebrate predators may lead to varying effects on prey populations: the density of prey may increase and reproductive success may improve (e.g. Marcström et al. 1988, Korpimäki and Norrdahl 1998, Norrdahl and Korpimäki 2000, Kauhala et al. 2000), the behaviour of prey may change (e.g. Norrdahl and Korpimäki 1998a, b, Banks et al. 2000), or the removed predator may be replaced by another predator (Henke and Bryant 1999). If one predator in the total predator assemblage is reduced, the effect of manipulation may not be obvious on prey populations because the remaining predator species may compensate for reduced mortality losses via decreases in interspecific competi-

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tion and intra-guild predation (Korpimäki and Norrdahl 1989, 1998, Norrdahl and Korpimäki 1995). Predator removal may lead to a decrease in the diversity of the prey species due to increased competition, e.g. for food (Sinclair and Norton-Griffiths 1982).

Removing predators to protect bird populations can have a large positive effect on hatching success, fledging success and post-breeding population sizes, but positive effects on the breeding density in the next year may still remain undetectable (Côté and Sutherland 1997). Unexpected effects inducing reductions in some prey species may also be possible, because the population of a competitively superior prey species may increase as a response to predator removal (Sih et al. 1985).

The American mink *Mustela vison* Schreb. is a medium-sized mustelid species from North America that was introduced to Finland for fur-farming in the 1920s. Escaped mink from fur-farms established free-living populations and spread in the early 1950s (Westman 1966). In the 1970s feral mink had spread all over the country, including Lapland and the outer archipelago (Kauhala 1996). Predation by feral mink may have caused local declines in bird populations in Finland, Sweden and Scotland, but experimental tests with large-scale manipulations of feral mink densities are still lacking. On the basis of observational data, detrimental impacts of feral mink have been documented on populations of some gulls (common gull *Larus canus* L., black-headed gull *Larus ridibundus* L.), terns (e.g. common tern *Sterna hirundo* L.), and auks (black guillemot *Cepphus grylle* L. and razorbill *Alca torda* L.) (e.g. Olsson 1974, Hario et al. 1986, Andersson 1992, Kilpi 1995, Craik 1997, Hario 2000). In the outer archipelago of the Baltic Sea, American mink is the only mammalian predator subsisting mainly on birds during the breeding season (Niemimaa and Pokki 1990), so the impact of mink predation may have similar detrimental effects as introduced predators have on the native fauna on oceanic islands (Groombridge 1992). Feral mink is a generalist carnivore that in winter mainly subsists on fish and small rodents, but birds are the principal prey in spring and summer (Gerell 1967, Wise et al. 1981, Dunstone and Birks 1987, Niemimaa and Pokki 1990). Besides dietary flexibility, the lack of natural competitors or enemies is probably an important factor affecting the success of the mink in the Baltic Sea archipelagos (Kauhala 1996, Väisänen et al. 1998).

We studied the effects of removing feral mink on breeding waterfowl populations in the archipelago of the Baltic Sea, SW Finland. We compare changes in breeding densities between two removal and two control areas, and show that many but not all waterfowl populations strongly increased as a response to mink removal.

Material and methods

Study area

The study was conducted on small islands of the Archipelago Sea, SW Finland (Fig. 1) in two phases: bird census was carried out from 1993 to 2001 in the mink removal area in Nauvo (R1) and from 1994 to 2001 in the control area in Dragsfjärd (C1). In the second phase, from 1998 to 2001, the study was extended with one more removal and control area, both in Korppoo (R2, C2). These areas consist of small islands and islets; rocks and skerries (von Numers 1995: p. 18), which are exposed, open rocky sites and with sparse vegetation (Tables 1 and 2). On the smallest islands there are only tiny patches of grasses and meadows, while on the larger islands junipers *Juniperus communis* L. develop uniform colonies and trees (mainly Scots pine *Pinus sylvestris* L. and mountain ash *Sorbus aucuparia* L.) are scarce and solitary. Small ponds are common, and they are of high importance for some ducklings.

The mink removal area in Nauvo (R1) (centre of the area 59°49′N, 21°48′E) covers 72 km^2 and consists of 60

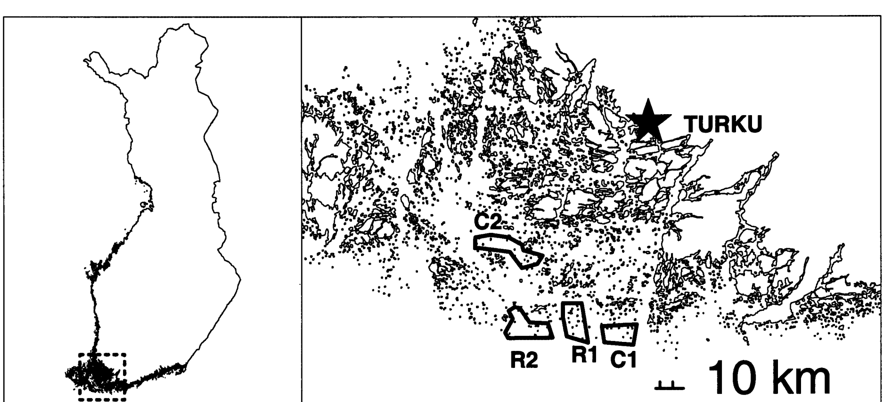

Fig. 1. Location of study areas in the Turku archipelago in SW Finland (R1 = removal area in Nauvo, C1 = control area in Dragsfjärd, R2 = removal area in Korppoo, C2 = control area in Korppoo). (National Land survey of Finland, permission no. 264/MYY/01.)

Table 1. Distribution of maximum height of the islands in the two removal (R1 and R2) and two control (C1 and C2) areas.

Maximum height (m)	R1 (%)	C1 (%)	R2 (%)	C2 (%)
<2.5	3.3	2.7	9.7	4.7
2.5–4.9	30.0	56.7	21.0	48.4
5.0–7.4	40.0	24.3	33.8	28.1
7.5–9.9	13.3	5.4	22.6	17.2
>10.0	13.3	10.8	12.9	1.6
Number of islands	60	37	62	64

islands (total land area 115 ha) and the control area in Dragsfjärd (C1) (59°48′N, 22°11′E) covers 35 km^2 and consists of 37 islands (total land area 57 ha) (Fig. 1). The removal area in Korppoo (R2) (59°47′N, 21°30′E) covers 125 km^2 and consists of 62 islands (total land area 108 ha) and the control area in Korppoo (C2) (60°01′N, 21°23′E) covers 130 km^2 and consists of 64 islands (total land area 107 ha) where birds are breeding. There are no obvious differences in the altitude and size of the islands between removal and control areas (Tables 1 and 2); nearly 75% of the islands are < 2 ha in size in all study areas. Islands are mainly rocky, only ca 10% of island areas are stony or sandy. No permanent human settlement is found in any area and all four areas belong to the joint working area of the Archipelago National Park (Finnish Forest and Park Service).

Mink removal

Feral mink were removed by two gamekeepers with a trained hound. An air-blasting device was used to flush mink from refuges below stones and dense clumps of junipers, and a shotgun was used to kill mink (Nummelin and Högmander 1998, Högmander 2000). Removal took place in autumn and again in spring just before birds had started to breed.

Removal of feral mink in the manipulation area in Nauvo (R1) started in autumn 1992. During the first autumn and spring before the bird census started, a total of 63 mink was killed, with number of removed mink later being considerably lower. A total of 98 mink was removed from autumn 1992 to spring 2001 (Fig. 2).

Table 2. The size distribution of the islands in the two removal (R1 and R2) and two control (C1 and C2) areas.

Area (ha)	R1 (%)	C1 (%)	R2 (%)	C2 (%)
<0.5	11.7	24.3	9.7	12.5
0.5–0.99	26.7	24.3	38.7	26.6
1.0–1.9	38.3	24.3	27.4	32.8
2.0–3.9	11.7	21.6	11.3	21.9
4.0–7.9	8.3	5.4	12.9	4.7
>8.0	3.3	0	0	1.6
Number of islands	60	37	62	64

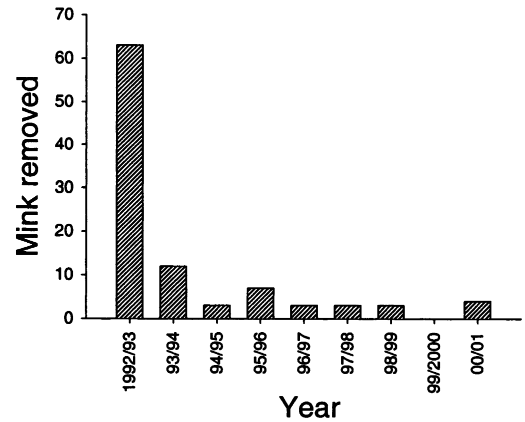

Fig. 2. Number of feral mink removed from the manipulation area in Nauvo (R1) before each breeding season (autumn/spring) during 1992–2001.

Out of 90 mink removed from autumn 1992 to autumn 1997, 37 were females (21 adults, 16 juveniles and subadults) and 53 were males (25 adults, 28 juveniles and subadults) (Laanetu and Nummelin unpubl.). On some occasions mink had re-invaded islands during the bird breeding season, but these individuals were rapidly removed. In addition two red foxes *Vulpes vulpes* L. and one raccoon dog *Nyctereutes procyonoides* Gray were also removed. Lethal IHJÄL-traps were used during winter on islands which might constitute bridges for new mink entering the area. In the removal area in Korppoo (R2) mink were hunted extensively from autumn 1998 onwards using the same methods, but trapping was a more important method in this area. Trapping was performed in particular from December to April on the inhabited islands, Utö and Jurmo, just outside the study area and from where mink may be dispersing. From autumn 1998 to spring 2001, 50 mink were removed from this area and its buffer zone. In the removal area in Korppoo (R2) evidence for mink presence was found on a few islands both in 1999 and 2001. In both cases it is probable that only one mink was involved. In 2000 a female with a juvenile was found in the north-western part of the area. In the first removal area (R1) mink removal started before the bird census started, but to replicate the initial part of the long-term mink removal bird census was started prior to mink removal in the second removal (R2) and control (C2) areas.

In the control area in Dragsfjärd (C1), we collected data during bird census on mink observations, scats, and prey items killed and stored by mink under rocks and junipers. During 1996–2001 we found some evidence for the occurrence of feral mink on $> 60\%$ of the islands of the control area (C1), including the outermost rock which is 2.1 km from the nearest island. In the control area in Korppoo (C2) signs of mink were found on 50% of the islands. We considered that feral mink were widespread and abundant in the control areas during the study (Laanetu and Nummelin unpubl., Miettinen unpubl.). We do not see any reason not to assume that the densities of mink in both removal and control areas have been more or less the same prior to the initiation of mink removal. Because mink move a lot between islands during open water (Niemimaa 1995), it is difficult to estimate the total number of mink or fluctuations in the population.

A total of 2922 scats of feral mink was collected in our study areas during 1992–1997. Forty-two percent of the samples consisted of fish, 32% of birds (mainly common eider *Somateria mollissima* L.) and 13% of mammals (mainly field vole *Microtus agrestis* L.). The remaining 13% consisted of amphibians, insects, molluscs and plants. The occurrence of birds in the diet was highest in spring and summer, while fish was the main food in winter (Laanetu and Nummelin unpubl.).

Other species that prey on ducklings, nestlings and eggs in our study areas are the great black-backed gull *Larus marinus* L., herring gull *Larus argentatus* Pontoppidan, hooded crow *Corvus corone cornix* L. and raven *C. corax* L.. The white-tailed sea eagle *Haliaeetus albicilla* L. is a daily sight in the study areas, while eagle owl *Bubo bubo* L. bred in the removal area in Nauvo (R1) in 1999 and 2001 but is uncommon in the other study areas. Scats left during winter by red fox were occasionally found in all areas, and by raccoon dog in areas R1 and C2.

Censuses of birds

Breeding birds were censused three times each breeding season from 1993 onwards in the removal area in Nauvo (R1) and from 1994 onwards in the control area in Dragsfjärd (C1). In 1998 bird census was started in the new removal and control areas in Korppoo (R2, C2). In early May, focus was on the mute swan *Cygnus olor* Gmelin, greylag goose *Anser anser* L., goosander *Mergus merganser* L. and common eider, in early June on mallard *Anas plathyrhynchos* L., shelduck *Tadorna tadorna* L. and tufted duck *Aythya fuligula* L., and in early July on late breeding velvet scoter *Melanitta fusca* L. The methods mainly follow the detailed instructions given by Hildén (1964) and Hildén et al. (1991) on censuses of archipelago birds. In short, numbers of the mute swan, the greylag goose and the common eider are based on nest counts. The population sizes of the other species are based, besides on nest counts, on the occurrence of broods or a pair in a suitable habitat. In mallard a lone male, a lone female or a pair was interpreted as one pair, but in the tufted duck with a clear surplus of males (Hildén 1964) only the pairs and females were interpreted as pairs. Clearly migrating individuals or a group of moulting ducks were not included.

Data analysis

We used a general linear model with a homogeneity-of-slopes analysis to test the effect of treatment (removal or control; the class variable) and year, which was the covariate, on the density of breeding birds. The interaction between year and treatment was the object of our primary interest. Density of pairs km^{-2} land area was the dependent variable in the model. We used the procedure GLM in the SAS statistical package (SAS 2000) ver. 8.1. The main results achieved in this study are from the long-term removal and control areas (R1 and C1), whereas the data from the second removal and control areas (R2 an C2) cover just four years. Therefore, these results should be interpreted as replicates of the experiment from the initial phase of the first removal and control areas (Figs 3–5).

Results

In the first removal and control areas (R1 and C1), mink removal had positive effects on the breeding densities of mallards, tufted ducks, velvet scoters and shelducks (Fig. 3 and Table 3). The breeding density of the mallard decreased steeply in the last study year 2001 (Fig. 3), and therefore, the treatment-year interaction is not significant for this species. However, this interaction is significant when considering the years 1993–2000 only ($F_{1,11}^{(treatment \times year)} = 7.69$, $p = 0.018$). The breeding densities of mallards and velvet scoters in the first year of the study in the removal area were both 0.87 pairs km^{-2} (per land area), and no tufted ducks bred. Breeding densities of mallards were highest in 1999 with 17.39 pairs km^{-2}, but thereafter they decreased to 5.22 pairs km^{-2} (Fig. 3), while breeding densities of tufted ducks were between 17 and 25 pairs km^{-2} during 1996–2001 (Fig. 3). Densities of velvet scoters increased to 34.78 pairs km^{-2} in 2001 (Fig. 3). The breeding density of shelducks increased as well, from zero pairs in 1993 to 3.5–4.3 pairs km^{-2} in 1999 to 2001 (Fig. 3). The increase in breeding populations of mallards, tufted ducks and shelducks was steepest during the 4–6 first years after the initation of mink removal whereas the increase in the breeding population of the velvet scoter continued throughout the study. The breeding densities of these four species were zero in the C1-control area, except in 1998–2000 for mallards, in 2000 for velvet scoters and in 2001 for tufted ducks.

Of the breeding tufted ducks in the removal area (R1), 86.4% were found in colonies of common gulls and terns (including mainly arctic terns *Sterna paradisaea* Pontoppidan but also some common terns), and 2.9% were breeding on totally gull- and tern-free islands. Also mallards showed a slight tendency to breed in these colonies: 55.7% of them bred in tern-common gull colonies. Of the breeding velvet scoters, 31.5% were found in the tern-common gull colonies. Because of close association of these waterfowl species with gull-tern colonies, we also analysed the proportions of common gull and tern colonies (≥ 5 pairs) in removal and control areas (Table 4). In the first removal and control areas (R1, C1), the interaction of mink removal and year was significant ($F_{1,13}^{(treatment)} = 1.56$, $p = 0.23$,

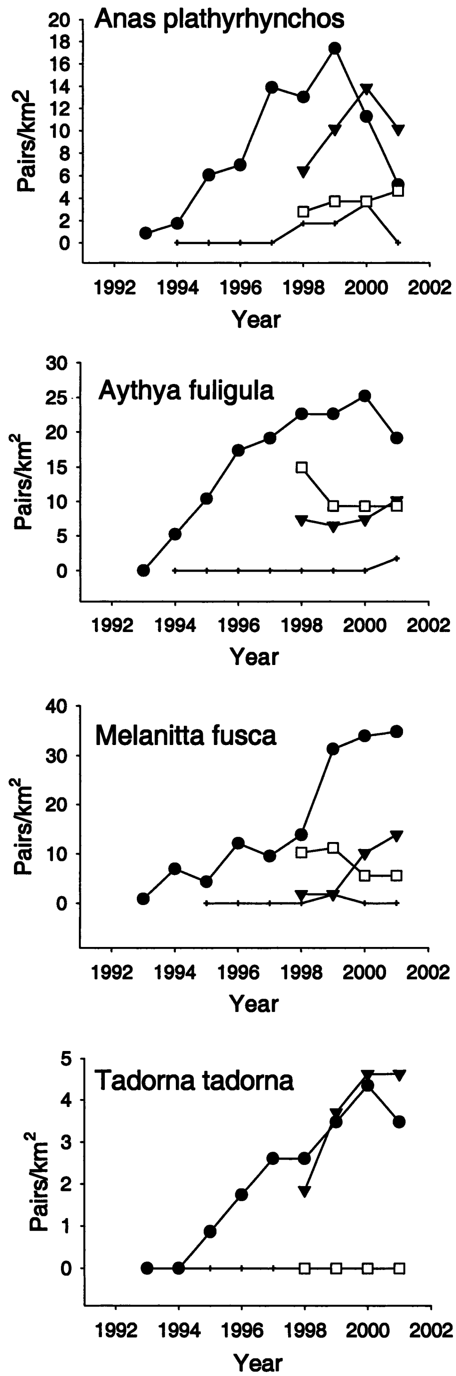

Fig. 3. Total densities (pairs km^{-2} land area) (from top) of mallards, tufted ducks, velvet scoters and shelducks in the mink removal (R) and control (C) areas in 1993–2001 (● = R1, + = C1, ▼ = R2, □ = C2). Mink removal started in autumn 1992 in R1 and in autumn 1998 in R2.

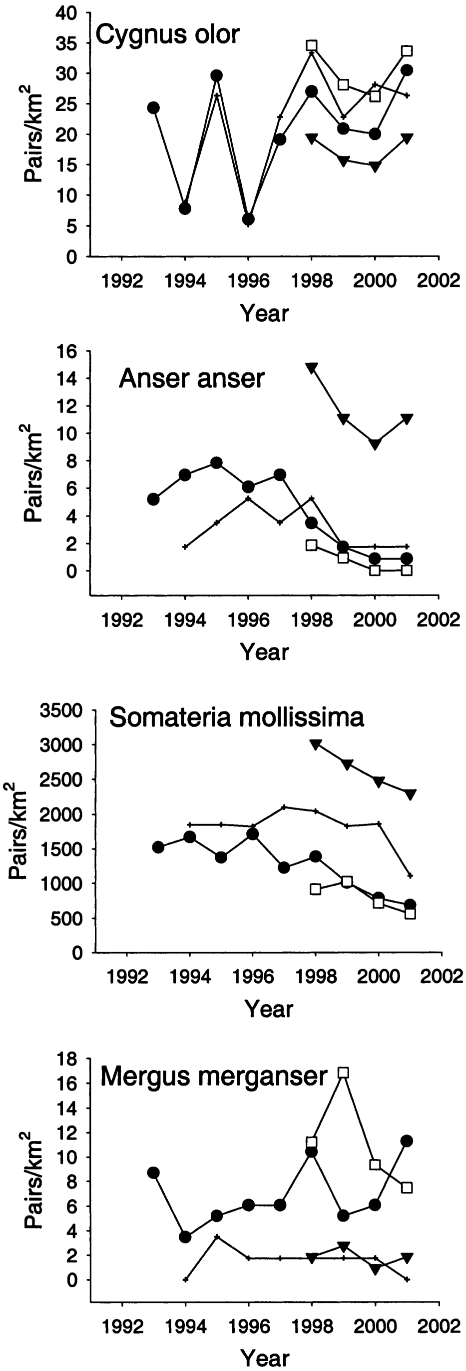

Fig. 4. Total densities (pairs km^{-2} land area) (from top) of mute swans, greylag geese, common eiders and goosanders in the mink removal (R) and control (C) areas in 1993–2001 (● = R1, + = C1, ▼ = R2, □ = C2). Mink removal started in autumn 1992 in R1 and in autumn 1998 in R2.

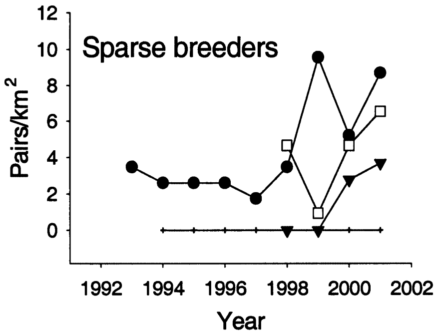

Fig. 5. Total densities (pairs km^{-2} land area) of the sparse breeders (pooled densities of gadwall, northern shoveler, pintail and red-breasted merganser) in the mink removal (R) and control (C) areas in 1993–2001 (● = R1, + = C1, ▼ = R2, □ = C2). Mink removal started in autumn 1992 in R1 and in autumn 1998 in R2.

$F_{1,13}^{(year)} = 14.84$, $p = 0.002$, $F_{1,13}^{(treatment \times year)} = 16.20$, $p = 0.027$), but in the second removal and control areas (R2, C2) it was not ($F_{1,4}^{(treatment)} = 4.07$, $p = 0.11$, $F_{1,4}^{(year)} = 0.42$, $p = 0.55$, $F_{1,4}^{(treatment \times year)} = 4.16$, $p = 0.11$).

For the two largest species, the mute swan and the greylag goose (Fig. 4), we found wide among-year variation in breeding densities in both removal and control areas. The among-year fluctuations in the breeding densities of mute swans were similar in removal and control areas without any obvious long-term trends. In years with high breeding densities, the population may be up to five times higher than during years with low breeding densities. A decreasing trend in the breeding densities of the greylag goose was evident.

The breeding densities of the common eider, the most abundant waterfowl in all study areas, were decreasing in all areas (Fig. 4). The goosander appeared not to respond to the mink removal (Fig. 4), and its density remained constant over the study period. The pooled numbers of sparse breeders, including gadwall *Anas strepera* L., northern shoveler *A. clypeata* L., pintail *A. acuta* L. and red-breasted merganser *Mergus serrator* L., increased also as a response to mink removal (Fig. 5).

In the second removal and control areas (R2 and C2), the velvet scoter and the shelduck showed significant increasing trends in breeding densities as a response to the manipulation (Table 3 and Fig. 3). These trends were also quite similar to the corresponding trends of the initial phase of the first removal and control areas. In addition, the breeding densities of mallards and sparse breeders also tended to increase in the R2 area as they did in the R1 area (Figs 3 and 5), whereas the increase for the tufted duck in R2 area remained unclear (Fig. 3). It should also be noted that the initial densities of many of the studied species were higher in R2 and C2 than in R1 and C1 areas. The

Table 3. ANOVA table for the effects of treatment (trt:mink removal and control), year (covariate) and their interaction on the breeding density for different bird species in the first and second removal and control areas (R1 and C1 vs R2 and C2). The sparse breeders include the gadwall, northern shoveler, pintail and the red-breasted merganser.

Species	Source	Removal 1 – control 1			Removal 2 – control 2		
		DF	F	p	DF	F	p
Anas plathyrhynchos	Trt	1	0.49	0.5	1	0.49	0.52
	Year	1	4.34	0.06	1	2.53	0.19
	Trt × year	1	1.67	0.22	1	0.5	0.52
Aythya fuligula	Trt	1	0.42	0.53	1	5.31	0.08
	Year	1	19.69	<0.001	1	0.44	0.54
	Trt × year	1	15.93	0.002	1	5.31	0.08
Melanitta fusca	Trt	1	1.97	0.27	1	21.25	0.01
	Year	1	37.52	0.18	1	3.17	0.15
	Trt × year	1	35.5	<0.001	1	21.25	0.01
Tadorna tadorna	Trt	1	2.3	0.15	1	9.74	0.04
	Year	1	59.9	<0.001	1	9.78	0.04
	Trt × year	1	59.9	<0.001	1	9.78	0.04
Cygnus olor	Trt	1	0.38	0.55	1	0.02	0.89
	Year	1	3.8	0.07	1	0.05	0.83
	Trt × year	1	0.52	0.49	1	0.02	0.89
Anser anser	Trt	1	5.48	0.04	1	0.5	0.52
	Year	1	10.44	0.007	1	4.78	0.09
	Trt × year	1	3.78	0.07	1	0.49	0.52
Somateria mollissima	Trt	1	1.11	0.31	1	2.99	0.16
	Year	1	14.12	0.002	1	38.2	0.004
	Trt × year	1	1.35	0.27	1	2.94	0.16
Mergus merganser	Trt	1	1.53	0.24	1	0.92	0.39
	Year	1	0.44	0.52	1	1.24	0.33
	Trt × year	1	1.37	0.26	1	0.92	0.39
Sparse breeders	Trt	1	0.19	0.67	1	0.17	0.7
	Year	1	5.16	0.04	1	3.92	0.12
	Trt × year	1	5.16	0.04	1	0.16	0.71

Table 4. Proportions (%) of islands that had common gull and tern colonies in each study area in 1993–2001.

Area	1993	1994	1995	1996	1997	1998	1999	2000	2001
R1	10.0	18.3	28.3	31.7	31.7	31.7	31.7	35.0	35.0
C1		8.1	10.8	13.5	10.8	10.8	18.9	13.5	10.8
R2						21.0	21.0	24.2	29.0
C2						25.0	28.1	18.8	23.4

mute swan, greylag goose, common eider and goosander showed similar trends in all four study areas during 1998–2001, even if the densities of the greylag goose and the common eider were notably higher in the R2 area than in the other areas (Fig. 4).

Pooled breeding densities of waterfowl species showed no response to mink removal, neither in the R1 and C1 areas ($F_{1,13}^{(treatment)} = 1.00$, $p = 0.33$, $F_{1,13}^{(year)} = 11.73$, $p = 0.005$, $F_{1,13}^{(treatment \times year)} = 0.98$, $p = 0.34$), nor in the R2 and C2 areas ($F_{1,4}^{(treatment)} = 2.32$, $p = 0.21$, $F_{1,4}^{(year)} = 37.82$, $p = 0.04$, $F_{1,4}^{(treatment \times year)} = 2.27$, $p = 0.21$).

Discussion

Species that have benefited from mink removal

Long-term removal of feral mink led to an increase in breeding densities of four of the species studied. For the tufted duck, velvet scoter and the shelduck the adult breeding densities increased from very low densities in the first two years after the mink removal began in the first removal area (R1). The same appeared to be evident for the mallard, even if the species decreased during the last two years of the study. The total breeding density of these species was less than one pair km^{-2} in the first year and the increase started in the following years. The trends in the second removal and control areas (R2 and C2) are consistent with these results, apart from the trends of tufted duck. The sparse breeders were absent in the first two years in the R2 area, but started to increase in the third and fourth year, and they increased in the R1 area as well, suggesting that mink may limit the overall diversity of waterfowl community.

In this study, feral mink have been able to live in an environment almost free from top predators and competitors. This phenomenon may somewhat resemble the "mesopredator release hypothesis" which states that densities of smaller mesopredators may increase considerably in an environment free from larger top-predators, and thus mesopredators may be able to severely limit their prey populations (Soulé et al. 1988, Courchamp et al. 1999). As the American mink is a generalist carnivore, it can maintain high densities even when some of the prey species are scarce, which may have contributed to its ability to severely reduce the densities of some of its prey species.

Tufted duck is known to show a strong attraction to breed in common gull and tern colonies, which has been well documented elsewhere (e.g. Hildén 1964, von Numers 1995). Consequently, one of the possible reasons for the increased breeding densities of tufted ducks, and also mallards, is the substantial increase of colonies of common gulls and terns in the first removal area (R1). Colonies of common gulls and terns may be safe sites to breed in because these birds defend their nests against large gulls and birds of prey, thereby also protecting other species from such nest predators. But the risk of nest predation by mink might increase because colonies are attracting mink, e.g. with their odour. In addition, a seabird colony can not effectively defend itself against a nocturnal predator and the otherwise protective colony may become vulnerable at night (e.g. Wendeln and Becker 1999). Another advantage to breeding in a colony is that it may decrease the individual's probability of being attacked; a dilution of the predation risk is possible in a colony in comparison to solitary breeders (Inman and Krebs 1987).

Velvet scoters and tufted ducks began to increase as soon as one year after the initiation of long-term mink removal. Velvet scoter reaches maturity in its third calendar year and tufted duck in its second or third calendar year (Cramp and Simmons 1977). This increase was therefore not solely a result of improvement in the breeding success of the previous year, implying that these birds might have been attracted to the mink-free habitat. Similar results have been obtained in North America, where breeding densities and hatching success of some duck species have increased soon after the initiation of removal of smaller mesopredators (red fox, striped skunk *Mephitis mephitis* Schreb., raccoon *Procyon lotor* L. and North American badger *Taxidea taxus* Schreb.) (Duebbert and Lokemoen 1980). Ferreras and Macdonald (1999) documented that the presence of mink affected the breeding density of coots *Fulica atra* L. and the hatching success of coots and moorhens *Gallinula chloropus* L. They also suggested that coots and moorhens might avoid areas with high mink density.

The results from the first removal and control areas may however be biased by some methodological flaws at the initial stage of the experiment. The control area (C1) was established one year later than the removal area (R1), and no pre-removal data from breeding densities of waterfowl were collected. However, to repeat the initial phase of the mink removal experiment properly, new large removal and control areas were established in 1998 (R2 and C2). The results from these new areas are essentially similar for mallards, shelducks, velvet scoters and sparse breeders. Their breeding populations have quickly increased as a response to mink removal, whereas in control areas their populations have remained at the initial low level.

Species that have not benefited from mink removal

Removal of mink did not affect the breeding densities of mute swans, grey-lag geese, common eiders and goosanders. The among-year variation in the breeding densities of mute swans was similar in both long-term and short-term removal and control areas. Swans are probably capable of defending them against mink, although in some cases mink have been able to kill even adult mute swans (Miettinen unpubl.). Cold winters and consequently a widespread ice-cover seem to be one of the most important factors affecting the breeding densities of mute swans in the next season (Hildén and Hario 1993, Nordström unpubl.). Winters 1993/94 and 1995/96 were cold with widespread ice-cover in the archipelago and the breeding density in the following year declined distinctly. Greylag goose is also a large and sparse breeder, and our results suggest that the removal of mink does not have obvious effects on its population size.

The population of the common eider in the Baltic Sea in general and also in the Archipelago Sea has increased during the last fifty years and is now dense (Stjernberg 1982, Väisänen et al. 1998), although a decrease has been noted in the Finnish eider population during recent years (Tiainen et al. 2001). Common eider is the most abundant species in the Archipelago Sea with ca 30 000–40 000 pairs breeding within the joint working area of the Archipelago National Park in the middle of the 1990s (Miettinen et al. 1997). It is also a common prey species for feral mink and other predators in the archipelago and coastal areas (Hario and Selin 1989, Niemimaa and Pokki 1990, Sulkava et al. 1997). The reason why the breeding population of the common eider has not increased after mink removal may be in the fact that territoriality limits feral mink so that they can not reach densities sufficient to reduce the high breeding densities of common eiders. In high prey densities both the functional and numerical responses may set limits on the predation rate (Sinclair and Pech 1996). There are also several other factors including parasites (Hollmén et al. 1996), diseases (Hollmén et al. 2000) and food abundance (Öst and Kilpi 1997) that may limit common eider populations and thus reduce the importance of predation. Gerell (1985) found that common eider females bred successfully in the presence of permanent mink occupation, but breeding success was low on islands only occasionally visited by mink.

Even though we have shown that mink removal may increase the breeding densities of many waterfowl species, there was no obvious effect on the pooled waterfowl breeding densities. This is a result of minor response of the eider breeding population to mink removal, but it also suggests that mink removal may not increase the overall abundance of waterfowl, even if the diversity is positively affected.

Conclusions

We have shown that predation by feral mink in the outer archipelago of the Baltic Sea can have at least locally limiting effects on the breeding densities and community structure of waterfowl. The breeding densities of some smaller species have drastically increased in mink removal areas whereas in control areas their populations have remained at the same initial low level. In contrast, the populations of larger waterfowl species did not show obvious increases in breeding densities after mink removal. Colonies of common gulls and terns seem to have a key position for some smaller waterfowl species, and the increase of tufted ducks, but also mallards, as a response to mink removal may be via the increase of gulls and terns. Additionally, it is only those species whose densities were close to zero that have increased, implying that the mink had severely limited their population densities, even close to local extinction. Furthermore, we suggest that at least for some of the species studied, the increase in the breeding population may not be a cause of improved breeding success, but simply that birds have chosen mink free islands where the predation risk is low (see also Martin 1993).

Our results also show that it is possible to remove feral mink from large areas of the outer archipelago and even maintain the area mink-free for several years with effective game-keeping. This has been facilitated by the fact that the area and islands are rather isolated, meaning that dispersion and re-colonisation of mink is slower than on the mainland. This study has shown that the populations of some, but not all, breeding birds may increase as an outcome of removing a main predator. Earlier studies indicate that predator removal does not generally increase the breeding population of birds, but island and insular ecosystems are most convenient to succeed in achieving increases in breeding densities of prey populations (Marcström et al. 1988, Côté and Sutherland 1997, Macdonald et al. 1999, Norrdahl and Korpimäki 2000, Kauhala et al. 2000, but see also Tapper et al. 1996).

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