Alien mink predation induces prolonged declines in archipelago amphibians

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Amphibians are undergoing enigmatic global declines variously attributed to a complex web of anthropogenic forces. Alien predators pose a fundamental threat to biodiversity generally that is predicted to be most acute in island ecosystems. While amphibian eggs and tadpoles are vulnerable to aquatic predators, the effect of predators on adult, reproducing frogs, which most influence amphibian population processes, is unknown. Here, we report on the responses of amphibian populations in the outer Finnish Archipelago to a long-term, large-scale removal of American mink (*Mustela vison* Schreb.), an invasive predator linked to recent biodiversity loss across Europe. Removal increased both the densities and distribution of common frogs (*Rana temporaria* L.) but not those of common toads (*Bufo bufo* L.), which appear to escape mink predation because of their unpalatable skin. Importantly, the largest benefits of mink removal to frog recovery were slow to appear as frogs apparently have a delayed maturation in these harsh environments, which means we must be cautious about reliance upon short-term results.

Keywords: *Bufo bufo*; delayed maturity; island populations; *Mustela vison*; predator removal; *Rana temporaria*

1. INTRODUCTION

Recent drastic population declines of many amphibian species across the world (Blaustein & Wake 1990; Wake 1991; Houlahan *et al.* 2000; Green 2003; Stuart *et al.* 2004) now make amphibian conservation an international biodiversity priority. Anthropogenic forces such as habitat loss and over-utilization, global climatic change, chemical pollution, acid precipitation (low pH), ultraviolet (UV-B) radiation, diseases and interactions with invasive species, are suggested as possible local causes (Blaustein & Wake 1990; Pasanen *et al.* 1998; Kiesecker *et al.* 2001; Pounds 2001; Kats & Ferrer 2003). Yet unidentified processes threaten 48% of rapidly declining amphibian species (Stuart *et al.* 2004). Alien predators pose a fundamental threat to biodiversity generally (Vitousek *et al.* 1997) that is predicted to be most acute in island ecosystems (Schoener & Spiller 1996; Courchamp *et al.* 2003). In the disappearance of oceanic island vertebrates since ca 1600, 34 of the 110 avian species' extinctions (31%) have been attributed to introduced mammalian predators (Groombridge 1992), while 81% of the 65 mammalian extinctions during the same period also occurred on islands (Ceballos & Brown 1995). Amphibians may be especially vulnerable to alien predators because adults are relatively immobile with few defences, while larval and juvenile phases are confined to pools. Alien predators have been linked to declines in larval growth and survival (Kats & Ferrer 2003; Vredenburg 2004), but the effect of

predators (native or alien) on adult, reproducing frogs, which most influence amphibian population processes (Vonesh & De la Cruz 2002), is unknown.

Feral American mink (*Mustela vison* Schreb.) is possibly the greatest predation threat for vertebrate biodiversity in Europe, being linked to a wave of drastic declines and even local extinctions behind their invasion (Nordström *et al.* 2002, 2003; Macdonald & Harrington 2003). The mink is a 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 & Harrington 2003). The mink is a semi-aquatic generalist carnivore that subsists mainly on fish, birds, small rodents and crustaceans, but also preys on amphibians throughout the year (Dunstone & Birks 1987; Niemimaa & Pokki 1990; Jędrzejewska *et al.* 2001). The importance of amphibians for mink depends on the availability of other food items in the environment they live (Gerell 1967; Jędrzejewska *et al.* 2001). As a generalist carnivore, mink may also eat frog eggs; both Day & Linn (1972) and Tolonen (1982) found mink with their stomachs full of frog spawn, but no remains of adult frogs which suggests direct predation on the spawn.

We studied the effects of American mink predation and island characteristics (isolation, size and availability of pools) on the abundance of two species of amphibians (common frog *Rana temporaria* L., and common toad *Bufo bufo* L.) subsisting on small islands in the outer archipelago

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of southwest Finland, Baltic Sea. The study comprised two mink removal areas (R1 during 1993–2001 and R2 during 1998–2001) and two comparable control areas (C1 and C2) each consisting of 60–77 islands (figure 1; Nordström *et al.* 2002, 2003). This large-scale replicated long-term field experiment offered a unique opportunity to resolve the impacts of mink on amphibian populations at appropriate spatial and temporal scales.

2. MATERIAL AND METHODS

(a) Study areas

This study was conducted in four areas in the central part of the Baltic Sea, southwestern Finland (figure 1). Each area covered 72–130 km², of which between 1.07 and 1.27 km² comprised small islands and islets. The mean island size in all areas was smaller than 2 ha. They were exposed, rocky sites and with sparse vegetation. The smallest islands had only patches of grasses, while on the larger islands junipers (*Juniperus communis*) constitute the major vegetation type. Small freshwater pools are numerous on most islands, and are of high importance for amphibians as their breeding sites. The number of suitable pools for amphibians varied between years due to climatic factors, and thus we counted the minimum number of suitable pools on each island. Island isolation was qualified by distance to nearest neighbouring island and number of islands within 2 km. We excluded unsuitable islands that lacked freshwater pools, as well as small (less than 1 ha) isolated islands (with pools but without appreciable vegetation) further than 1 km from nearest vegetated, larger island. This limit distance was chosen because such islands were inhabited by frogs only within 600 m of another (larger) island. We assume that, in comparison to the mainland, these harsh outer archipelago islands offer unfavourable conditions for amphibians as there is less food and are fewer refuges and alternative prey for their predators.

(b) Predator removal

Mink were removed annually during autumn and early spring by gamekeepers using a trained hound to find them. Mink were flushed from refuges using an air-blasting device and then shot. During 1992–2001, 98 mink were removed from R1 (of which 63 were removed during the first autumn and spring), and during 1998–2001 *ca* 50 individuals from R2 (see details in Nordström *et al.* 2002). Only a few re-colonizing individuals were found in removal areas during breeding seasons and they were rapidly removed. In all areas, we noted any signs like scats, prey remains or mink tracks. Out of the examined 3068 scats and 62 mink stomach contents from our study areas, 2.3% contained remains of common frogs (Laanetu and Nummelin 1992–1997, unpublished work) and no toad remains. We assumed that mink densities in control areas were comparable to pre-removal conditions (see Nordström *et al.* 2002, 2003). Birds (dabbling ducks, waders, gulls, corvids) and snakes (mainly the black adder, *Vipera berus*) also prey on amphibians, and invertebrate predators take eggs and tadpoles in our study areas. But populations of many dabbling duck species, waders and gulls markedly increased in the mink removal areas in comparison to control areas (Nordström *et al.* 2002, 2003), which cannot account for major increases of common frogs in mink removal islands.

Figure 1. Location of the two removal (R1, R2) and two control areas (C1, C2) in the Finnish SW archipelago (National Land Survey of Finland, permission no. 829/MYY/04).

(c) Amphibian populations

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). However, egg strings may be mixed into each other leading to a possible slight underestimate of common toads (Laurila 1998). 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). The smooth newt (*Triturus vulgaris*) is the only other amphibian species present in the areas.

(d) Statistical analyses

We analysed our data using a generalized linear model with negative binomial distribution in the GENMOD procedure of SAS-statistical software (SAS Institute Inc. 1999, pp. 1363–1464). Observations from years 1998–2001 were analysed together, accounting for islands with multi-year data using a repeated measures analyses (in procedure GENMOD using generalized estimation equations). Due to gaps in the data, observations for common toad were missing for R2 and C1 in the year 1998, and for R1 in the year 2000. For common frogs, observations were missing for R1 for the year 2000. During year 2001 only common frog observations in parts of R1 and C1 were collected. Common frog observations from R2 for spring 1998 were also removed from the analyses because removal did not start in this area until that autumn. The full model included number of egg batches (common frog) or egg strings (common toad) as response variable, with area (R1, R2, C1 and C2), survey date, year, island size, number of pools, number of islands within two kilometres and distance to closest island as explanatory variables. We used area instead of treatment because the two removal areas have been treated for different time-periods and we wanted to detect time-scale effects of the experiment. Clearly non-significant variables from the initial models were dropped from the final models (table 1a).

Table 1. (a) Effects of explanatory variables on the number of female common frogs and toads per island (generalized linear models; GENMOD) and (b) contrast effects of pairwise comparisons between each study area for the number of female common frogs and toads per island (generalized linear models; GENMOD).

	common frog		common toad	
	χ^2	<i>p</i>	χ^2	<i>p</i>
(a) explanatory variable				
area	36.22	<0.0001	10.33	0.016
survey date	7.42	0.0064	5.33	0.021
year	9.48	0.024		
island size (hectares)	10.02	0.0015	5.89	0.015
number of pools per island	3.50	0.062		
number of islands within 2 km	3.33	0.068		
(b) contrasts				
R1–C1	35.87	<0.0001	7.90	0.005
R1–C2	15.42	<0.0001	4.34	0.037
R2–C1	6.49	0.01	6.16	0.013
R2–C2	0.94	0.33	2.87	0.09
R1–R2	9.71	0.002	0.29	0.59
C1–C2	5.36	0.021	0.02	0.88

3. RESULTS

The long-term mink removal had an obvious effect on common frogs. In 1998–2001, female frogs were significantly more numerous per island in the long-term mink removal area (R1) than in the short-term removal area (R2) and in two control areas (C1 and C2; figure 2a, table 1a,b). Numbers of females in the short-term removal area (R2) differed significantly only from one control area (C1; figure 2a, table 1a,b). In R1, the number of female frogs increased annually by 46% during 1993–1998, but from 1998 to 1999 their numbers increased by 462% and from 1999 to 2001 the increase was still 119% (figure 2b). In addition, the proportion of islands occupied by common frog females in R1 increased from under 50% to over 90% during 1993–2001 (figure 2b).

However, mink impacts were complex, because while toads were generally less abundant than frogs, they appeared unaffected by alien mink. Common toad females were found less in R1 than in the two control areas, and in R2 less than in one control area (C1; figure 2a, table 1b). Besides the differences between areas, there were a number of other factors affecting both frog and toad numbers (table 1a). Both frogs and toads were more abundant on large islands than on small ones, but island isolation (number and total area of islands within 2 km, and distance to the closest island) and number of pools per island did not have significant effects on numbers of females (table 1a). Survey date did affect the numbers of both species. Egg batches and strings were found less frequent with later survey date, apparently because of egg predation and pool desiccation.

4. DISCUSSION

Our results clearly show that predation by an introduced mammalian predator may have drastic detrimental effects on population densities of frogs and induce prolonged

Figure 2. (a) Number (least square means and 95% confidence limits) of common frog and common toad females per island in two removal and two control areas. For frogs, the model includes area (R1, R2, C1 and C2), year (1998–2001), survey date (from 25 April to 21 May; number of egg batches decreased with later survey date), island size, number of pools per island and number of islands within 2 km as explanatory variables (see also table 1a). For toads, the model includes area, survey date, and island size, respectively (see also table 1b). (b) Total number of common frog females per island (circles) and proportion of islands occupied (triangles) in the long-term mink removal area (R1) in 1993–1999 and in 2001. The same 33 islands were surveyed in 1993–1999 (filled symbols), of which only six were surveyed in 2001 (open symbols).

declines in island amphibians despite their low importance in the diet of the predator. Importantly, the greatest positive effect of mink removal on frog populations took seven breeding seasons to appear, apparently because of the delayed maturation of common frogs. Thus the huge increase observed in the seventh spring occurred due to the maturation of the first common frog generation born after mink removal. That was the first year in which the number of reproducing individuals was not restricted by predation. Common frog females first reproduce at the age of 2 years in favourable environmental conditions, whereas reproduction is delayed in unfavourable conditions, such as in the north or at high altitudes, until the age of 5–6 years (Elmberg 1990; Miaud *et al.* 1999). Also the harsh conditions in the outer archipelago seem to delay the maturation of the frogs. In theory, it is also possible that some other predators of frogs (e.g. some waterfowl, adders) slowed the frogs' population increase until year seven and then suddenly disappeared, but this seems unlikely as there was no evidence of big fluctuations in the abundance of these predators.

Unlike common frogs, common toads have unpalatable skin (Laurila 1998), which presumably protects them from alien mink predation. At forested riversides of eastern Poland the otter (*Lutra lutra*) preys on common frogs but also on common toads, while the American mink

only preys upon frogs in the same habitats (Jędrzejewska *et al.* 2001). Mink is nonetheless capable of eating toads after skinning them, but probably does so only in extreme circumstances, such as lack of other food (M. Ahola 2001, personal observations). The observed higher number of toads in the control area could reflect an advantage of toads due to selective predation by mink on these two anuran species. But these unexpected differences might also be due to the location of the study areas in relation to larger islands. The common toad lays larger clutches and thus needs larger breeding pools than the common frog (Laurila 1998). Accordingly, as the large pools are mainly found on the large islands, the most abundant toad populations also live on them (M. Ahola 1994–2001, personal observations). For toads the small islands in our study areas probably represent marginal habitat and these toad populations may be sink-populations which are dependent on the source-populations inhabiting the larger islands outside our study areas. There are a number of large islands in the vicinity of both control areas, whereas the removal areas are a bit more isolated from the larger islands (figure 1), which may explain the between-treatment difference in the toad numbers.

This large impact on frogs was only revealed by a unique long-term experimental study, where population recovery, as a result of investment in feral predator control, took many years to appear. Hence, the threat posed by advancing alien predators to amphibian populations may have been previously underestimated, and could be one reason why many amphibian populations have shown enigmatic declines even in otherwise pristine environments (Stuart *et al.* 2004). In areas with patchy habitat distributions, like archipelagos with small islands, alien predator impacts can be serious, even on populations of secondary prey species. Our earlier results show that mink removal increases (i) the breeding densities of the main prey of mink, seabirds; (ii) the number of species (species richness) of archipelago birds (Nordström *et al.* 2002, 2003; Nordström & Korpimäki 2004); and (iii) densities of voles (Banks *et al.* 2004). It appears then that the detrimental and disruptive consequences of feral mink predation may impact on the entire island vertebrate community with cascading consequences to the whole archipelago ecosystem.

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