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The American mink: the triumph and tragedy of adaptation out of context

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Abstract The American mink has spread widely beyond its native North America due to the activities of fur traders. The mink is an extremely adaptable, generalist predator. Over two continents, the American mink is associated with problems in the conservation of local species because of their impact on both prey and competitors. Here, we review the impact of American mink on native species, stemming from over a decade of research, and concentrate on two examples: the impact of American mink on the water vole in Britain and on the European mink in Eastern Europe. While the near extinction of the water vole in Britain and that of the European mink in Eastern Europe are largely due to predation and interspecific aggression, respectively, both may have been affected by a multitude of factors acting synergistically. Terns, and other seabirds, are impacted by mink predation; the effect on riparian bird species is less clear but may potentially be high. Emerging principles, supported by preliminary evidence, suggest that the return of the larger otter in the United Kingdom may be detrimental to mink populations. The impact of, or on, the current recovery of the polecat in the United Kingdom is unknown but evidence from Eastern Europe suggests that American mink negatively affect at least female polecats. We conclude by briefly presenting two case studies of small-scale mink removal and discuss considerations for future control projects. To mitigate mink impact on a larger scale we suggest a holistic approach, involving mink removal, habitat restoration, and recovery of native competitors.

Keywords alien species; American mink; competition; invasive species; *Mustela*; predation; predator removal

INTRODUCTION

Since the early work of Paul Errington (Errington 1946) on mink and muskrats in the United States, the American mink has been influential in science. Errington's findings on the ecology of predation, and predator-prey population dynamics, challenged contemporary anti-predator policies and is now a classic study cited in undergraduate textbooks. More recently—and ironically carried out initially through fur farms; the source of this invasive species—the focus of research has been on the unusual reproductive physiology of the mink and its implications for mating systems and spacing patterns (Yamaguchi et al. in press; Johnson et al. 2000). Female mink exhibit both superfecundation (multiple ova from a single ovulation) and superfoetation (multiple ovulations within a single mating season; Shackleford 1952; Venge 1973); two adaptations that, when females mate with multiple males (Thom et al. in press a), result in multiple paternity of litters (Shackleford 1952; Venge 1973; Yamaguchi et al. in press). Although the exact benefits of polyandry and of litters of multiple paternity are unclear, there are potentially many (Jennions & Petrie 2000; J. Wolff & D. W. Macdonald unpubl. data). Further, paternity analysis of wild litters suggests that, in contrast to existing theories on the relationship between male reproductive tactics and space use (Emlin & Oring 1977; Powell 1979; Sandell 1989), male residency may not be in any way associated with fatherhood (Yamaguchi et al. in press). Mink are also unusual

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among other mustelids in that although they exhibit delayed implantation, the time period is extremely short (up to only 35 days; Mead 1981; Sandell 1990; Thom et al. in press b). In fact, this short delayed implantation in mink is suggested to be the mechanism that facilitates superfoetation (Shackleford 1952; Yamaguchi et al. in press).

The adaptability of this small, semi-aquatic mustelid is manifest by its widespread colonisation over two continents. Its proliferation, and resulting impact on native species, clearly owes much to its comparatively great fecundity (Macdonald et al. 2002a), although exactly how the mink's unusual reproductive system affects their place within the guild of semi-aquatic mustelids is unknown. However, while the biologist in us marvels at the success of the American mink and delights at the challenge of understanding its adaptations, the challenge it sets to conservationists and ethicists is both daunting and distressing.

Originally found only in North America, the mink has spread widely beyond its native range, having been introduced inadvertently or deliberately by fur traders into South America and Europe. Initially they were brought to Europe in the 1920s for fur farming: first to France, then to Sweden in 1928, to Norway and the United Kingdom in 1929, and to Denmark and Iceland in 1930. Between 1933 and 1963 they were also deliberately released into the wild in the former Soviet Union to establish a harvestable population (Heptner et al. 1967). Considerable numbers were involved in such releases; in the years up to 1971 the releases of 20 400 mink at over 250 sites were documented (Pavlov & Korsakova 1973). The result of deliberate releases, coupled with escapes from fur farms, is that the American mink is now widely established as an invasive species in Iceland, Scandinavia, the former USSR, Germany, France, Spain, and the British Isles (Wildhagen 1956; Gerell 1967a; Westman 1968; Aliev & Sanderson 1970; Cuthbert 1973; Smal 1988; Birks 1990; Birks & Dunstone 1991), and as far afield as Patagonia, Argentina (Previtali et al. 1998).

Wherever American mink go they are associated with problems in the conservation of local species, because of their impacts on both their prey and their competitors. The most thoroughly researched examples are of the impact of American mink on the water vole in Britain (Macdonald & Strachan 1999) and on the European mink in Eastern Europe (Macdonald et al. 2002a). However, there is a long list of other candidate negative impacts of mink introductions, which includes concerns that they threaten the Eiderdown harvest in Iceland (Bjornsson & Hersteinsson 1991), and the conservation of both endemic rodents and mustelids in Argentina (Previtali et al. 1998; Aued et al. in press). Perhaps the greatest scrutiny of the impact of American mink on native wildlife has been in Britain (Linn & Chanin 1978; Birks 1990; Birks & Dunstone 1991; Clark 1991; Lawton & Woodroffe 1991). Here, ground-nesting birds in both freshwater systems (Smith 1988; Ferreras & Macdonald 1999) and in the marine environment of offshore islands may be at risk (Craik 1990, 1993, 1995, 1997). Burrow-nesting shelduck are vulnerable to the arrival of mink on islands in Loch Lomond (Bignal 1978); puffins and shearwaters are likely to be similarly at risk. The decline of white-clawed crayfish may also be accelerated by mink predation (Smal 1991).

Although the wide distribution of introduced American mink has undoubtedly had an undesirable impact on local communities, it also serves as a natural experiment, providing the opportunity to investigate ecological theory to an extent that would otherwise be neither practical nor ethical (Macdonald & Thom 2001; Macdonald et al. 2001). Furthermore, the possibility of manipulating introduced carnivores (e.g., during control operations) offers the opportunity for studies of predator-prey and interspecific competition systems (Boitani 2001), which are not only of fundamental importance but also of practical significance. This review stems from over a decade of research by several members of our team, in both the United Kingdom and abroad, in which fundamental questions are addressed with the aim of contributing to the management of the American mink and the conservation of those species in danger of extinction as a result of its introduction. For more details, see Macdonald & Strachan (1999) and Macdonald et al. (2002a).

IMPACT ON PREY

Mink are generalist predators that will feed on fish, invertebrates, birds, amphibians, and small mammals (e.g., Gerell 1967b, 1968; Akande 1972; Eberhardt & Sargeant 1977; Chanin & Linn 1980; Birks & Dunstone 1984; Ben-David et al. 1997). In their native North America the mammals consumed by mink are predominantly muskrats and hares, replaced by rabbits, brown rats, and field voles in the United Kingdom (Dunstone 1993; Strachan & Jefferies 1996a). However, the proportion of mammals in the diet, and indeed, of individual prey species, varies significantly with local availability and abundance. Thus, mink diet may differ between individuals (Sidorovich et al. 2001), between sexes (Dunstone 1993; McDonald 2002) and between seasons (Sidorovich 2000a).

Water voles in lowland England

The devastating decline of the water vole in Britain was initially documented by Strachan & Jefferies (1993) who carried out the first nationwide survey, covering 2970 localities, in 1989–90. Although almost half of these sites (48%) revealed occupancy by water voles, comparison with earlier records suggested that only 32% of sites occupied by water voles before 1939 were still occupied. The survey not only confirmed the suspected decline of the water vole (Jefferies et al. 1989) but also suggested that the rate of decline had accelerated through the 1980s and 1990s. The situation has continued to deteriorate, and in 1999 the English population was estimated to have declined by a further 80%. The following summary is drawn largely from Macdonald & Strachan (1999).

Several hypotheses were put forward to explain the apparent plummeting of water vole populations. These included natural causes (i.e., disease and predation) as well as anthropogenic causes associated with habitat loss, degradation or fragmentation, through changes in land use, fluctuations in water levels associated with land drainage, and pollution. Agricultural intensification, unsympathetic riverside management, and an escalating intensity in land use over the last decade, especially in southern England, has eroded and often obliterated the riverside habitats preferred by water voles. Concurrent with this revolution in land use, the American mink has spread throughout the United Kingdom system of waterways. The fact that water voles have an apparently innate fear of American mink odour (Barreto & Macdonald 1999), and that the anti-predator adaptations of these voles are ineffective against American mink, boded badly.

Whilst naturalists observed that the arrival of mink coincided locally with the disappearance of water voles, the pioneering establishment of a quantitative relationship between the two species came from Woodroffe et al.'s (1990) study on the Yorkshire moors. The changing distribution of the two species on the Thames catchment also provided a vivid illustration; the spread of mink within the catchment providing an incriminating mirror image to the decline of water voles (Fig. 1; Barreto et al. 1998a). Indeed, in 1995, no water vole signs were found at sites populated by mink, and there were no signs of mink at any site where water voles persisted. A less extensive but more detailed study along 20 km stretches of four rivers in the Thames catchment demonstrated a negative correlation between the numbers of mink caught and the numbers of water vole signs (Halliwell & Macdonald 1996).

Scats (faeces) are a reliable, and relatively easily found, sign of mink presence (Bonesi & Macdonald in press). Assuming that mink are unlikely to be regularly active more than 1 km beyond the sites where their scats are abundant, and in an attempt to test for an association between the disappearance of water voles and the movements of mink, Strachan et al. (1998) recorded water vole latrines in 17 × 200 m sectors of the River Soar (Leicestershire) categorised as either low or high mink presence. It was assumed that sectors of high mink presence were subject to frequent foraging by resident mink (successful breeding dens were found in at least two), while those of low mink presence were subject to only occasional foraging by transients. Indeed, they found that the mean monthly occurrence of water vole latrines was lower within the mink's zone of influence than beyond it (Fig. 2). Male mink are particularly mobile during the spring rut (Yamaguchi & Macdonald in press) and mink signs were prolific in February and March. Thereafter, with the birth of kits in May, mink signs were less widely dispersed until late summer, when the female and her kits began to radiate further afield from their breeding dens. At this time, there was a concomitant reduction in water vole signs.

To investigate the time scale of these effects, Strachan et al. (1998) divided the study area on the River Soar into two 600-m sections; one where the mink were in their first year of occupancy, the other where they had been resident and breeding for 2 years. They found that by the late spring of the first year in which mink had bred on a stretch of river, water vole signs were rare. In the second year site, high water vole sign counts in the spring of the first year of the study crashed to only two latrines in August and September, and no latrines at all by October. During the following year of mink occupancy, a single latrine with only two droppings was found in March. Further small-scale studies have documented the complete disappearance of a water vole colony within a few months of a single mink arriving there (Barreto & Macdonald 2000; T. Moorhouse pers. comm.).

So, do mink over-harvest water voles? In a study of American mink diet on 11 rivers in Derbyshire,

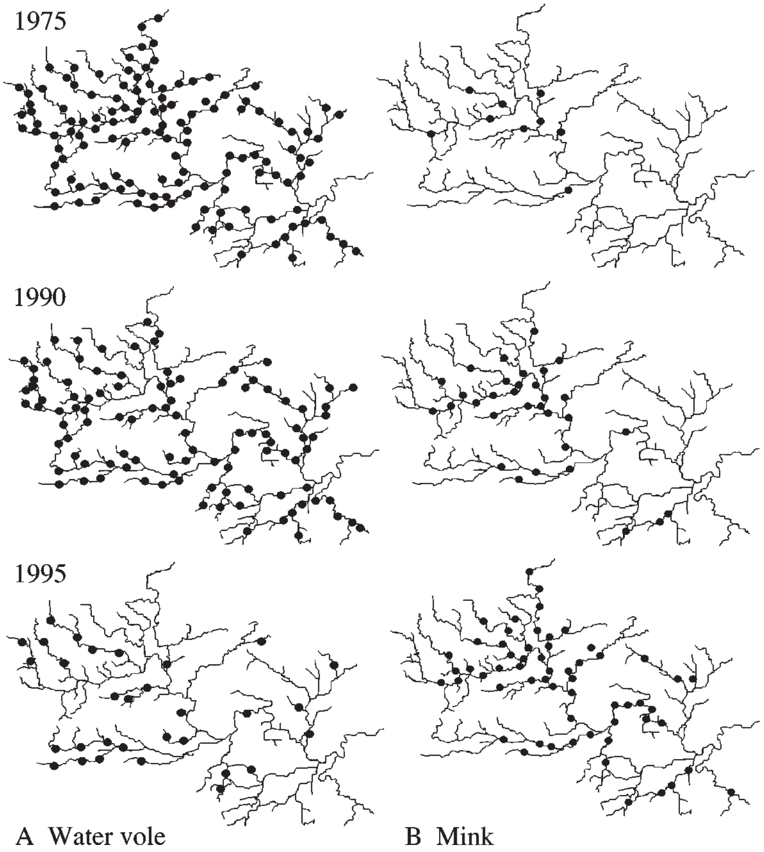


Fig. 1 Sites at which water voles and mink were recorded in the Thames catchment, southern England, in each of 1975, 1990, and 1995. Of 130 sites in the Thames catchment known to support water voles in 1975, only 95 had water voles in 1990, and by 1995 only 31 did so: these figures suggest that an average loss of 2.33 known sites per annum between 1975 and 1990 had accelerated to 12.8 sites per annum between 1990 and 1995. In 1975 only 9 of 30 sites revealed signs of mink, this had increased to 32 by 1990 and to 60 sites by 1995. Reproduced from Macdonald & Strachan (1999).

Leicestershire, Staffordshire, and Nottinghamshire, Strachan & Jefferies (1996a) showed that the water vole was the single most important species in the diet of colonising mink. Indeed, in the May/June sample they comprised up to 32.2% of the volume of undigested prey remains. While this observation might seem at odds with studies that have reported water voles to be rather infrequent prey (Day & Linn 1972; Chanin & Linn 1980; Birks & Dunstone 1984; Dunstone & Birks 1987; Ireland 1990), it is likely that the latter studies were conducted in areas where water voles were already uncommon—possibly due to the earlier impact of mink. That their importance as a dietary item declines as their populations are depleted was demonstrated on the River Soar (above) where a significantly greater bulk of water voles (as % dry weight) were eaten in the first year of mink occupancy than in the second (Strachan et al. 1998).

While not conclusive evidence, these studies suggest that the long-term relationship between mink and water vole may be a classic example of a prey being insignificant to a predator's population, while the predator is pivotal to the prey's population (Erlinge et al. 1984). They demonstrate that, not only can mink cause water vole extinction at a local level, but also that this could happen within 2 years (with dramatic reductions, even extinction, possible within a single mink breeding season). Furthermore, the disappearance of water vole signs as young mink emerge from their den suggests that the female mink and their young are the main agents of destruction. Male American mink occupy ranges that overlap those of several females and some males may range over as much as 9 km of river even during the relatively immobile non-mating season (Yamaguchi & Macdonald in press). Yet the disappearance of water voles on the River Soar was apparently concentrated in stretches of 2–4 km, suggesting a key role for the female. Female mink, being approximately half the size of males (Dunstone 1993), may be especially effective hunters of water

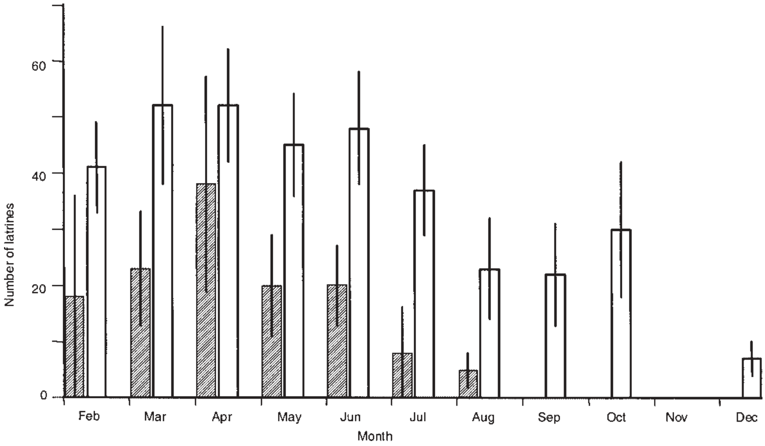


Fig. 2 Number of water vole latrines in 200 m sectors of the River Soar (Leicestershire, England) designated as either high (hatched bars) or low (open bars) mink presence (n = 10 and 7, respectively). Reproduced from Strachan et al. (1998).

voles, in that they, but not male mink, can squeeze into the vole's burrows.

As in upland streams (Lawton & Woodroffe 1991), the presence of mink appeared to be the most important factor determining water vole distribution in the Thames region, explaining more of the variance in the data than did any other habitat variable recorded (Barreto et al. 1998b). Barreto et al. (1998b) also revealed two important changes in the relationship between water voles and their habitat as mink abundance increased. Firstly, water vole presence was positively correlated with the presence of submerged vegetation and vegetated bars at high mink density. These features provide water voles with food and refuges against predators, perhaps because mink are unlikely to pursue prey in vegetated waters where visibility is poor and access restricted. Secondly, the presence of water voles was related to water quality when mink were at high density, whereas no such relationship was detected in a previous survey when mink density was lower. Areas of high water quality characterise good fisheries, which in southern England are subject to intense mink control. It is possible, therefore, that water voles are found in these areas because mink are not. This would be another example of declining species being pushed to habitats negatively related to their agent of decline, rather than positively related to itself (Caughley 1994).

Evidence from the Highlands of Scotland suggest that there American mink may be the sole cause of water vole extinction (Lambin et al. 1998; Aars et al. 2001); this unitary explanation is, however, unlikely to hold universally (Lever 1978; Linn & Chanin 1978; Chanin 1981a; Birks 1990). Other, mutually compatible hypotheses include habitat degradation and fragmentation, fluctuations in water level, pollution, and disease, and these led Barreto et al. (1998a) to conclude that while none were exclusive, all might act synergistically. On this basis, Barreto et al. (1998a) proposed the tightrope hypothesis, which states simply that water voles have been constrained to a narrow and fragmented ribbon of habitat: a tightrope from which they will fall if nudged by any or all of a variety of factors. The mink is just one such factor.

If the tightrope hypothesis is correct then there is a possibility that habitat recreation in the long-term could act to mitigate the impact of American mink. There are, for example, areas of wetland in the southern United Kingdom where mink and water voles have coexisted for more than 20 years (Barreto et al. 1998b). Carter & Bright (2003) also suggest that reedbeds provide water voles with a refuge from mink predation. The optimal abundance, configuration, and dispersion of water vole habitat is not clear, however, nor is it necessarily intuitive. In the pristine wetlands of Belarus, Macdonald et al. (2002b) found that surviving enclaves of water voles were associated with isolated and small (less than 15 m in diameter) blocks of habitat: areas that may be too small to sustain resident American mink. Such isolated populations, however, are extremely vulnerable to stochastic processes, and all the more so for species, including water voles, that are poor dispersers (Stoddart 1970). Rushton et al. (2000), for example, concluded that water vole populations in some areas are now so fragmented that they may not be viable even in the absence of mink predation. Rushton et al. (2000) used an individual-based, spatially explicit model and demonstrated that extinction becomes more likely as both habitat fragmentation and mink predation increase, with mink predation effectively doubling the probability of extinction over that arising from fragmentation alone at all levels of fragmentation. Furthermore, isolated habitats are less likely to contain water voles simply as a function of the greater distance to neighbouring source populations (Lawton & Woodroffe 1991; Tefler et al. 2001; Bonesi et al. 2002). Such considerations aside, it is uncertain whether in areas of apparent coexistence, coexistence can continue indefinitely or whether we are simply observing a slower extinction rate. Individual process-based models provide a powerful tool for exploring these questions and devising restoration strategies (Macdonald & Rushton 2003). Although quantitative evidence is lacking, a reduction in the proportion of water vole in the diet of both American and European mink in Belarus since the invasion of the American mink suggests that, even in pristine wetland ecosystems, American mink limit water vole numbers (Macdonald et al. 2002b).

Birds

Through the 1990s American mink have seriously affected the nesting success of several ground-nesting bird species on the west coast of Scotland (Craik 1990, 1993, 1995, 1997). Blackheaded gulls (*Larus ridibundus*) have declined by 52%, common gulls (*Larus canus*) 30%, and common terns (*Sterna hirundo*) 37%, with lesser declines in other species such as eider (*Somateria mollissima*), red breasted merganser (*Mergus serrator*) and oystercatchers (*Haematopus ostralegus*). Many tern and gull colonies in the Oban area have been deserted or wiped out (Craik 1993). Like many carnivores, mink will kill more birds than they can eat (Kruuk 1964), storing the surplus to eat later. Up to a hundred birds may be killed in one night. In Iceland, one mink den was found to contain over 200 guillemot chicks (T. Björnsson pers. comm.). The eggs, young, and sometimes also the adults, are vulnerable to predation (Craik 1990).

Clode & Macdonald (2002) investigated the impact on terns of the American mink's southerly colonisation of the Hebridean archipelago in 1992–93. At the time mink were common throughout the northern islands of Harris and Lewis (Angus 1990) and present on some of the islands in the Sound of Harris, but were not found on the Isle of Uist or the islands further to the south. This situation presented an ideal natural experiment, and Clode & Macdonald (2002) were able to compare tern breeding behaviour in mink-inhabited and in mink-free areas. One particular problem in assessing the impact of mink on terns is the high level of variability in tern abundance and distribution between years (Thom 1986). Thus, whereas the total number of pairs in Lewis, Harris, and the Sound of Harris combined fell from 1678 in 37 colonies in 1980 to 359 pairs in 14 colonies in 1993, surveys in 1999 revealed more pairs (2183) in fewer colonies (21) than in 1980. Colony distribution in the Sound of Harris was not correlated with mink distribution; colony size, however, was greater in the northern (mink-inhabited) islands compared with the southern (mink-free) islands.

One might speculate that larger colonies mean greater vigilance and protection of numbers (cf. Bertram 1980; Foster & Treherne 1981) and indeed, terns do apparently learn something about the threat posed by American mink with exposure (terns, but not larger gulls, responded more vigorously to mink models on islands occupied by mink; Clode et al. 2000). Whether or not this has a direct effect on breeding success, however, is not so clear: variation between colonies was high, and no difference was detected in breeding success (measured as number of chicks per pair) between colonies (Clode & Macdonald 2002). Nevertheless, summing data across all colonies, revealed a general trend for higher productivity in mink-free areas (0.23 chicks per pair in four mink-free colonies versus 0.12 chicks per pair in three mink-inhabited colonies). A later survey by Rae (1999) similarly found reduced fledging success in mink-occupied colonies.

Perhaps of greatest conservation concern is the spread of mink to the more southern islands of the Hebridean archipelago, which provide some of the most important wader breeding grounds in Europe (Moore et al. 2003). These areas contain 25% of the United Kingdom breeding populations of ringed plover (*Charadrius hiaticula*) and dunlin (*Calidris alpina*), two species that are believed to have declined through the 1990s (Fuller & Jackson 1999). The decline in breeding birds on the Uists is usually ascribed to the arrival of hedgehogs (*Erinaceous europaeus*) in 1974, or to common gulls or hooded crows (*Corvus corone*) (Jackson & Green 2000), but invading mink (or indeed ferrets) could have played a role. Our team surveyed North Uist in 1999 and confirmed the widespread presence of American mink (Harrington 2003); among the mink caught that year were breeding females (L. Harrington unpubl. data) suggesting that mink could have been present on the island for longer. Furthermore, the decline in waders was most marked on Berneray, a small island off the north-east coast of North Uist that is a likely first landing point for mink crossing the Sound of Harris (Harrington 2003; see Moore at al. 2003).

Whether mink predation has an effect on riparian bird species was initially more controversial than their effect on seabirds, and early studies produced contradictory results (Lever 1978; Linn & Chanin 1978; Smith 1988; Halliwell & Macdonald 1996). Analysis of mink predation on waterbirds on the Thames, however, suggested that the impact differs between bird species (Ferreras & Macdonald 1999). Ferreras & Macdonald (1999) demonstrated that while both the abundance and breeding success (proportion of eggs hatched) of coots (*Fulica atra*) was negatively related to mink abundance (taking account of habitat), there was no relationship between mink abundance and either the abundance or the breeding success of moorhens (*Gallinula chloropus*). Coots nest on the water surface, usually among emergent vegetation (Chanin 1981b) whereas moorhens often build their nest on branches of trees and shrubs above water level (Taylor 1984). Therefore, coots’ nests are likely to be more vulnerable to predators, such as mink, foraging along the bank-water interface. In general, however, the proportion of waterfowl in mink diet is related to waterfowl density and may be particularly intense during the breeding season. Ferreras & Macdonald (1999) estimate that mink predation may be responsible for the mortality of 30–51% of adult coots (50–86% coot clutches) and 16–27% of adult moorhens (46–79% of moorhen clutches). While these figures are subject to numerous assumptions, they do indicate that nest predation on both coots and moorhens may be high. Nevertheless, there was no indication that mink resident in the Thames region limited the abundance of either coots or moorhens. This result confirms a survey of mink and moorhen abundance in the same area by Halliwell & Macdonald (1996) and accords with conclusions of both United Kingdom (Chanin & Linn 1980) and United States (Eberhardt & Sargeant 1977) studies.

IMPACT ON COMPETING PREDATORS

The presence of alien American mink not only impacts their prey but may also affect the entire guild of semi-aquatic predators into which they have been introduced. Species within such guilds do not usually overlap in terms of size (whether this is measured as absolute body size or size of fundamentally important morphological features, such as canines). The driving force behind such character displacement is still the subject of some debate (e.g., Dayan & Simberloff 1996, 1998; Dayan et al. 1989, 1990; McDonald 2002) but is most widely accepted to be the result of interspecific competition. This raises the question then: what happens when an alien species, very similar in size to one of the native ones, is introduced? Dayan & Simberloff (1994) found marked community-wide character displacement for canine diameter among British and Irish mustelids, and suggested that the American mink might be taking over the vacant niche of the heavily persecuted polecat (*Mustela putorius*; the mustelid to which the mink was morphologically most similar in Britain). In the former USSR, the spread of the American mink is associated with the decline of the European mink (see Maran et al. 1998a).

The European mink

The European mink is convergent with the American mink through its shared semi-aquatic habits, but although the two mink species are so similar in appearance and ecology that they were originally considered to be subspecies (Ognev 1931; Heptner et al. 1967; reviewed in Novikov 1939; and Ternovskij 1977), they are not closely related. The American mink is, in fact, a taxonomic outlier in the genus *Mustela*, and the European mink is closely related to the European polecat (Youngman 1982; Masuda & Yoshida 1994; Davison et al. 1999, 2000a,b). Historically, the European mink was widespread throughout Europe, with a range that extended from the Ural mountains to eastern Spain and from Finland to the Black Sea (Novikov 1939; Heptner et al. 1967). Since the 19th century, however, its range has dwindled drastically (reviewed in Maran et al. 1998a). There is now no known large population of European mink surviving in the wild; their decline is continuing, and the species retains only isolated fragments of its former range in small areas of France and Spain, north-eastern Belarus and restricted parts of Russia. In contrast, over the same time period, other semi-aquatic mustelids in the area appear to have either held their own (polecat), or decreased far less dramatically (otter, *Lutra lutra*, Foster-Turley et al. 1990), while the American mink has spread and substantially increased in number (Maran et al. 1998a). The following account is drawn largely from Macdonald et al. (2002a).

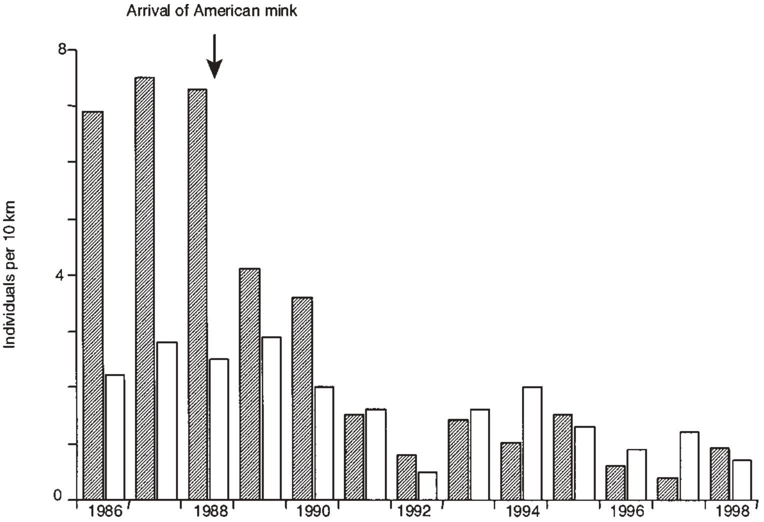


Fig. 3 European mink density on the upper reaches of the Lovat River, Belarus (winter 1986–98) in small rivers (hatched bars) and brooks (open bars). Small rivers defined as 5–25 m wide and 0.5–2.5 m deep (slow- and fast-flowing); brooks 0.5–2.0 m wide, 0.1–0.8 m deep. Brooks are often dry in the summer. The first American mink was trapped in the study area in December 1988; by spring 1990 it was common. Reproduced from Sidorovich & Macdonald (2001).

Various hypotheses were initially proposed to explain the decline of the European mink, including habitat loss, competition and/or hybridisation with the polecat, pollution, and over-hunting. While all were plausible, at least to some extent, none offered a single satisfactory explanation (Maran & Henttonen 1995; Maran et al. 1998a). The documented decline of the European mink on the Lovat River in north-eastern Belarus through the 1990s, coinciding with the arrival of the American mink in 1988, however, provided circumstantial evidence incriminating the American mink (Fig. 3; Sidorovich 2000b; Sidorovich & Macdonald 2001). Prior to the arrival of the American mink, between 1986 and 1989, European mink densities on small rivers ranged between 4 and 10 individuals per 10 km watercourse (mean = 7.3 per 10 km, SD = 2, n = 10); values that are high for this species (Novikov 1939; Danilov & Tumanov 1976). After the arrival of the American mink, between 1992 and 1995, maximum densities were less than two individuals per 10 km.

There are three main mechanisms (all of which are potentially linked) by which American mink may cause a decline in European mink, which are: competition for food, transmission of disease, and/or interspecific aggression. Hybridisation between European and American mink (which may result in non-viable embryos, Ternovskij 1977; Ternovskij & Ternovskaja 1994) appears to be out of the question as the chromosome number of the European mink is 38 and that of the American mink is 30 (Graphodatsky et al. 1976). Several features, however, suggest that in competition (whether this is competition for food or direct interspecific aggression) the American species might have the advantage. American mink are larger (American mink body mass, mean ± SE: male: 1310.2 ± 38.9 g, n = 42; female: 780.7 ± 21.0 g, n = 23; European mink: male: 976.6 ± 24.5 g, n = 14; female 667.0 ± 12.7 g, n = 8; Sidorovich et al. 1999). They are extremely adaptable (American mink appear to be able to utilise any body of water including artificial ones), and have larger litters than do European mink (mean 5.8 versus 2.4; Ternovskij & Ternovskaja 1994; see also Sidorovich 1993).

The hypothesis that American mink transmitted a fatal disease to European mink was not tested explicitly. However, various sources of anecdotal evidence do not support it. No signs of disease were observed among 258 European mink and 68 American mink housed in close proximity or over three separate behavioural tests during which up to eight individuals were exposed to direct contact with the other species (Maran 1989; Maran et al. 1998a). Although the absence of evidence of disease does not constitute evidence of absence, especially not in captive animals, there is no evidence of it in the wild either: over 4 years of radio-tracking in Belarus none of a total of 14 European mink succumbed to disease.

If competition for food does occur, we may predict that there would be a large overlap in diet between the two species, and that such competition would be especially significant over prey species that are scarce. Diet analysis, in north-eastern Belarus, revealed that although European mink diet was slightly more specialised than American mink, both species occupied a wide food niche, taking a spectrum of small mammals, amphibians, fish, and other prey. Overlap in their diet was indeed considerable (Sidorovich et al. 1998, 2001; Sidorovich 2000a; Fig. 4). The prey species that figured especially strongly in the zone of overlap, however, were rodents and frogs, yet there was no evidence that in Belarus either of these were scarce. Food competition for a scarce or declining resource, therefore, is not supported.

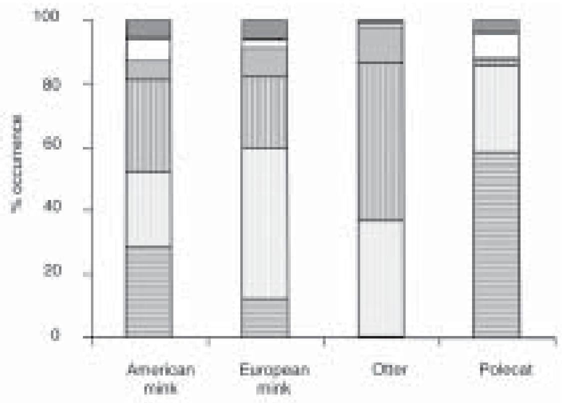


Fig. 4 Occurrence of prey types in faeces collected 1988–95 in north-eastern Belarus. Faeces only collected when positive species identification was possible from trapping, tracking or radio-tracking. Total faeces = 4312 (American mink 1930, European mink 1474, otter 641, polecat 267). All sites and seasons combined. Dietary overlap assessed using Pianka's index: European mink-American mink = 0.83; European mink-otter = 0.86; American mink-otter = 0.79; American mink-polecat = 0.78; European mink-polecat = 0.58; otter-polecat = 0.27. Prey types: horizontal lines = small mammals; dots = amphibians; vertical lines = fish; hatched = crustaceans; unfilled = birds/reptiles; shaded = other. Reproduced from Sidorovich et al. (1998).

By contrast, Maran et al. (1998b) found large differences in the diet of the two species in Estonia in the early stages of the American mink expansion (1984–90). Here, European mink ate a greater proportion of fish and crayfish and a smaller proportion of small mammals and amphibians than did American mink. Niche separation between the two species was far greater than that recorded in Belarus, but appeared to be due to differences in habitat use. Whereas American mink hunted in slow-flowing rivers, the European mink tended to hunt only in the upper reaches and fast-flowing waters. After the disappearance of European mink (in 1995), however, the diet of American mink in the same upstream area as previously occupied by the European mink was remarkably similar to that of European mink before. In other words, when choosing from the same spectrum of food availability, and in absence of other species, both American and European mink appeared to select largely the same food source (as was found in Belarus).

Two scenarios are compatible with these observations. The first is that the more specialised European mink occupied the fast-stream niche, which the American mink could not use until the European mink had gone for some unrelated reason. The second is that the American mink aggressively ousted the European mink from the slow-flowing river areas first, as that is its preferred habitat, and finally occupied all areas.

Support for the latter interpretation came from the Lovat River in Belarus, where densities of all semi-aquatic species before and after the arrival of American mink were recorded (Sidorovich 2000b; Sidorovich & Macdonald 2001). Before the arrival of American mink, the density of European mink was highest in small rivers, and lowest along brooks (Fig. 5). Otter density was highest in larger rivers. Polecats were found to inhabit all types of riverbanks and shores at similar density, but also used many other habitat types such as bogs, forested areas, and villages. No changes in habitat use by otters were found after the arrival of the American mink (see Fig. 5). Gradually, however, during 4 years of American mink expansion, European mink became rare in small rivers. Along brooks, used less frequently by American mink, there was less change. Polecat density was also reduced by about half in all riparian habitats. Concurrent with declines in density there was also a shift towards a male-biased sex ratio in both European mink and polecats (European mink before the arrival of the American mink: 1:1.6; after: 1:5.1; polecat, before: 1.5:1; after: 1:3.5 (1992–93), 1:10 (1994–96) and 1:18 (1997–98); Sidorovich 2000b). Similar sex ratio changes have been observed in the adjacent Pskov region of Russia (Danilov & Tumanov 1976). In European mink, at least, sex ratio changes may be associated with differential habitat use between the sexes, because females appear to use brooks (the habitat least affected by American mink) less often than do males (21.5% female radio-locations versus 51% male radio-locations recorded at brooks) but small rivers (a habitat where European mink are now rare) more often (60.7% radio-locations versus 20.2%; Macdonald et al. 2002a). It is possible that female European mink are unable to inhabit brooks continually because they have insufficient resources to allow them to raise a litter. Indeed, during the Belarussian field study, not one litter was found at small brooks, whereas 33 were found along small rivers and glacial lakes.

The idea of interspecific aggression was tested further in captivity. Indeed, behavioural observations of the two species in captivity suggested that American mink of both sexes were more aggressive to European mink than vice versa (Maran et al. 1998a). Given free, and simultaneous access to a large enclosure, European mink fled from American mink in 25% of male-male interactions, whereas American mink males fled from European males in only 3.4% of interactions. Similarly, in 17.0% of female-female interactions, American mink females chased the European mink whereas in only 2.2% of interactions did the European mink female chase the American. Five years of radio-tracking in Belarus suggested that aggressive encounters between American and European mink were also common in the wild (Sidorovich et al. 2000). In 56 cases when American and European mink were within between 200 and 1000 m of one another, aggressive encounters were recorded in 14. Furthermore, such encounters were almost always (in 13 of 14 cases) initiated by male American mink, and directed towards European mink of both sexes.

Given that size differences between sympatric species may be sufficient to reduce competition for resources (Ralls & Harvey 1985; Dayan & Simberloff 1994), Sidorovich et al. (1999) predicted that the arrival of the larger American mink in Belarus would initiate a divergence in size between American mink and European mink. On the contrary, they found a clear convergence. When American mink first appeared in the study area, they were significantly larger than both European mink and polecat (in both body weight and length). After the arrival of American mink, however, European mink of both sexes were substantially heavier and longer. There was some evidence that female polecats were also larger, yet American mink showed a general decline in body weight (Fig. 6). The first few American mink to be caught in the study area were remarkably heavy (first three males, mean mass = 1906.7 g; first two females, mean mass = 895.0 g). One possible explanation for this is that the larger individuals in a population are the most likely ones to emigrate and colonise new areas. Subsequently, this hypothesis has gained support by our finding that in the Hebrides, males in the recently colonised island of North Uist were heavier and larger than those in South Harris (the presumed source of the population; L. Harrington unpubl. data). Another possibility is that they are responding to local selection pressures. Similar increases in body size of European mink have, however, been recorded in Western Russia (Macdonald et al. 2002a)—Sidorovich et al. (1999) suggest that this may be due to reduced survivorship of smaller individuals, probably as a result of direct aggression from American mink.

There is increasing evidence of significant intraguild aggression among several carnivore species, including between American and European mink (in which females are particularly vulnerable due not only to their smaller size but also to their habitat preferences). However, it seems that European mink were already in decline before the arrival of the American mink (Tumanov & Zverjev 1986). Maran & Henttonen (1995) suggested a combined hypothesis, somewhat analogous to that proposed for the water vole (see above; Barreto et al. 1998a) i.e., that habitat loss, riparian engineering, pollution, and intense hunting all set in train the decline of the European mink, whereupon the American mink delivered the *coup de grâce*. This idea is simple and intuitively appealing, yet there are areas, such as in north-east Belarus, where the habitat remains wild and where, despite intensive trapping, American mink flourish and European mink are declining fast. Macdonald et al. (2002a), therefore, suggest that the spread of people and farming, rather than being a problem *per se*, may have historically favoured the polecat and consequently disadvantaged the European mink. They hypothesise that, more recently, the polecat has lost ground again with the degeneration of subsistence farming, and that had it not been for the arrival of the American mink the European mink might have reversed its fortunes.

This raises some interesting questions for the situation in England, where the recovery of European polecats is giving them the numbers to spread back into their former niche, which is now largely occupied by the American mink. It remains to be seen how these two species will interact and what the outcome will be, but our work in Eastern Europe suggests the prediction that female polecats may lose in aggressive encounters with American mink; an alternative possibility is that polecats may have a competitive advantage in the agricultural landscape of southern England. However, 21st century agriculture in the United Kingdom is vastly different from the non-intensive agriculture of Eastern Europe in the early 1990s, and heavy reliance on farmland can have other adverse effects (due to, for example, pesticide exposure; see Birks & Kitchener 1999; Harrington & Macdonald 2002). Our team is currently tackling these questions.

The otter

Within the guild of semi-aquatic predators of which the American mink is an introduced member, the relationship between the mink and the otter is especially interesting. At least superficially there is substantial overlap in the diet of these two species, but otters are considerably larger than American mink. A burgeoning literature from other carnivore communities has revealed the generality of hostility of larger carnivores towards smaller ones. An early example was the proposal by Hersteinsson & Macdonald (1992) that the larger red fox, *Vulpes vulpes*, harassed the smaller arctic fox, *Alopex lagopus*, and thereby limited the distribution of the latter. Many other examples have accumulated, as reviewed by Macdonald & Sillero-Zubiri (in press), who suggest that such hostility may be most fierce where niche overlap is greatest. On this basis one would predict that otters might be inimical to American mink (much as American mink are proven to be to European mink).

There is mounting evidence in support of this prediction. For example, in the Nahuel Huapi National Park in Patagonia, there is an inverse relationship between numbers of the endangered southern river otter (huillin, *Lontra provocax*) and American mink (Previtali et al. 1998; Aued et al. 2003). The mechanism in this case is as yet unknown, but both species consume predominantly crustaceans (80% mink diet, n = 60 scats, c. 99% otter diet) in the National Park, suggesting that competition for food is possible. Interestingly, at a smaller scale (i.e., within an individual lake) there is a positive correlation between the probability of finding huillin signs and the probability of finding mink signs. Both species appear to be using the same habitat (areas of deep water with overhanging vegetation associated with abundant crustaceans), thus increasing the possibility for, and probably the intensity of, interspecific competition.

In Britain, European otters are about seven times larger than American mink and therefore, might be expected to have the upper hand in interspecific competition. The first confirmation of this came from the Hebrides, where Clode & Macdonald (1995) studied the diet of both otter and mink on islands where the two species were sympatric and where they were allopatric. Both species changed their diet when in the presence of the other, yet the difference was not symmetrical. Otters did not alter their dependence on aquatic prey regardless of the presence of American mink. The diet of mink, however, became significantly more terrestrial when they coexisted with otters than when they did not (Fig. 7). There is evidence that similar shifts to a more terrestrial diet also occurs in lowland riverine systems as otter density increases (Bueno 1996).

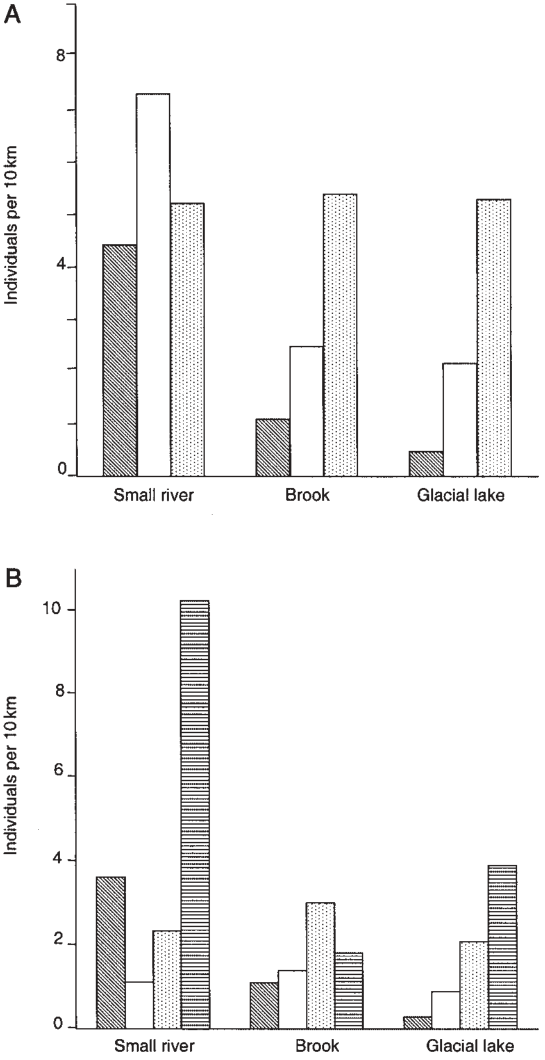


Fig. 5 Density of otter (hatched bars), European mink (open bars) and polecat (dots) **A**, before the expansion of the American mink: winter 1986–89; and **B**, when American mink was at high density (lined bars): winter 1992–95. Reproduced from Sidorovich & Macdonald (2001).

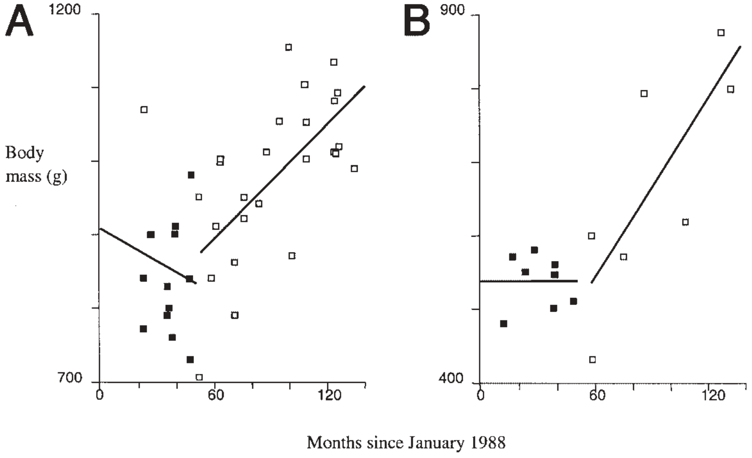
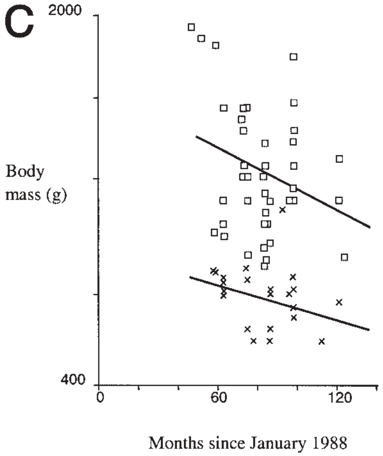


Fig. 6 Body mass of European mink: **A**, males; and **B**, females from January 1986 until February 1997, before arrival of the American mink (filled squares) and after (April 1990) (open squares); and **C**, of American mink males (squares) and females (crosses), after their arrival in the study area. Reproduced from Sidorovich et al. (1999).



Against this background, the current recovery of the otter in England provides an interesting opportunity to test the prediction that otters will disadvantage American mink, and also raises questions as to whether this might in turn limit the damage caused by mink to, for example, water voles. Following a widespread population crash, largely due to organochlorine use (Strachan & Jefferies 1996b), otter populations in England have, over the last few decades, increased and expanded their range considerably, recolonising many former habitats. From a low point of being found in only 5.8% of 2940 survey sites in the 1970s, by 2002 the species occupied 36.3% of national sites (Crawford 2003). Recovery is most pronounced in the south-west of England, where otters are now considered to be close to carrying capacity and fully recovered (R. Strachan pers. comm.). Here, field sign surveys for mink have recorded concomitant declines as otter signs have increased (Strachan & Jefferies 1996b; Bonesi 2003; Crawford 2003). Further, recent autopsied otters have been found to have bite marks on their lips believed to have been made by mink, suggesting direct interaction (V. Simpson pers. comm.). Recent work by our team supports the prediction of competition expressed as intra-guild hostility between otters and American mink in lowland English river systems (L. Bonesi & D. W. Macdonald unpubl.data). A further possible complication is the evidence of Aleutian disease in feral American mink in England (Yamaguchi & Macdonald 2001).

CONTROL OF AMERICAN MINK

Feasible options for mitigating the impact of American mink include: direct control of mink numbers, restoration and/or manipulation of habitat, and exploitation of the natural recovery of native predators. Logically, there is also the possibility that various non-lethal control methods might be utilised, whether these focus on exclusion (e.g., mink-proof fencing, equivalent to that which has been used successfully for pine martens, Balharry & Macdonald 1996), or on various types of repellent (e.g., Baker & Macdonald 1999).

Direct control: two case studies and future considerations

Theoretically, there are alternative methods whereby mink numbers could be selectively reduced. However, innovations such as virus-vectored immuno-contraception are not only far off but are also problematic in themselves (Bradley 1994;

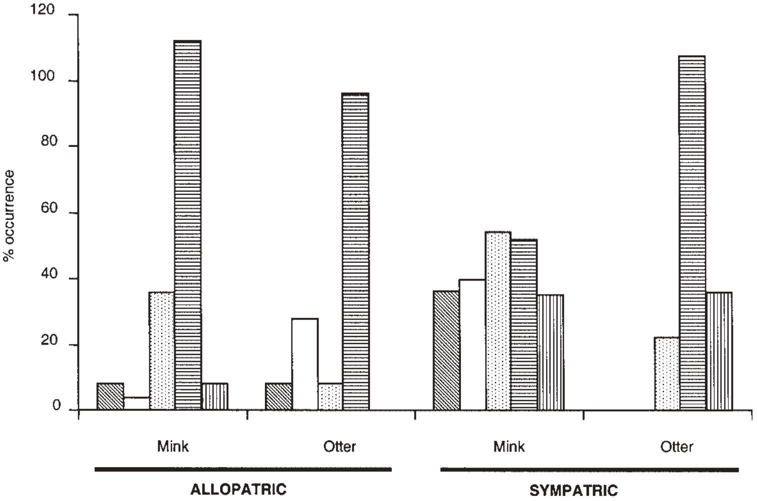


Fig. 7 Occurrence of prey types in faeces of American mink and otter in the Hebrides, United Kingdom, when allopatric and when sympatric. Prey types: hatched bars = small mammals; open bars = birds; dots = crustaceans; horizontal lines = fish; vertical lines = other. Reproduced from Clode & Macdonald (1995).

Tyndale-Biscoe 1994; Tuyttens & Macdonald 1998a,b). One practical option (and probably the only feasible one at present) is removal trapping, which, in the United Kingdom and in Belarus where there are other mustelids of a similar size, means live-trapping and selectively killing any American mink captured. The expense of such an operation on a large scale in the UK would be enormous (Macdonald & Strachan 1999). In Belarus, however, where there is an inexpensive rural labour force, the implementation of such a policy on a local scale is feasible. Here, we briefly summarise two case studies where removal trapping was used to mitigate the effect of American mink on the European mink (both are described in detail in Macdonald et al. 2002a).

Control of American mink in the Gorodok Nature Reserve (north-east Belarus) was initiated in 1992–93. Although it was clear that control would be effective only for as long as trapping effort could be maintained, the urgency of the situation warranted action. In a 20 × 30 km area, 70–80 American mink (an estimated 80% of the local population) were removed in the first year by one experienced biologist and local trappers. Without this intervention European mink would probably have disappeared from the area in the winter of 1995–96 (Fig. 8). In 1998, a further 73 American mink were captured between March and December. Since then low numbers (less than 40 in total) have been removed every autumn and in the spring of 2001. Local biologists are committed to continuing this programme indefinitely.

In an attempt to provide a more long lasting solution to the conservation of the European mink, Macdonald et al. (2002a) proposed the creation of island sanctuaries free from American mink. One such island (Hiiumaa Island, c. 1000 sq km including surrounding islets) was located in the Baltic Sea 22 km from the Estonian mainland. European mink were not present on the island, so a release of captive-bred individuals was planned. American mink, however, were present and so had first to be eradicated. Local support was crucial for this project, for both practical and ethical reasons, so 15 local hunters were recruited for the eradication. In the absence of European mink lethal traps could be utilised; Alaskan trappers recommended the "Conibear-type" trap in combination with commercially produced (United States) mink lures. These traps are set in tunnels or openings and are designed to kill instantly (it is also the only lethal trap that is legally permitted in Estonia). After the failure of the first trapping session in December 1998, however, when only seven mink were captured, the hunters requested (and were provided with) locally built wooden live-traps, which they deemed were more suitable for conditions on Hiiumaa. Mink lures were replaced by local fish bait. Success did not improve: only five mink were captured over 3 weeks in January and February.

At this point the task was passed to a field biologist with great experience in mink trapping and equipped with his own modified leg-hold traps, adapted to hold a captured animal without causing injury. On the basis of a snow-tracking survey of the entire island our team estimated that a maximum of 74 American mink was present. In fact, 45–65 traps throughout the island over three separate 1–2-month periods in 1999, brought the total killed to 50, after which intensive snow tracking in February and

March 2000 failed to reveal any signs of American mink (the last captive fur farm mink had been killed in 1998, and the isolation of the island made recolonisation unlikely). To date, more than 160 captive-bred European mink have been released on the island; although the first goal was to experiment with restoration techniques as a basis for future planning, preliminary results suggest that European mink are establishing on this island sanctuary.

Despite these localised successes, landscape-scale mink extermination has thus far proven to be impractical (Dunstone 1993; Boitani 2001). A notable example is the United Kingdom, where the Ministry of Agriculture, Fisheries and Food (now reconstituted within the Department of the Environment, Food and Rural Affairs), failed to eliminate American mink in the 1960s despite the capture of 5000 mink in England and Wales (King 1983). This failure was largely because the effort was too little and too late—and there is little evidence that it was carefully thought out. While the circumstances are changing, and the recovery of the otter may well work against the American mink, at least in lowland England, the recovery of the polecat (a protected species) will make mink trapping more problematic. There is no doubt that any attempt at wide scale American mink control in Great Britain will be difficult to achieve, will involve very labour intensive trapping, and will raise substantial welfare concerns (as discussed in Macdonald & Strachan 1999).

These issues are more manageable where attempted control is more localised (e.g., in the Hebrides, see Moore et al. 2003; or in important water vole refuges). However, the best operational strategy is not obvious and haphazard predator control has a discouraging record (see Macdonald et al. 2000). Planning should keep a firm grasp on the requirement that the benefit of attempted American mink control (e.g., lowered mink population and reduced risk to water voles and other native wildlife) must outweigh the costs (e.g., time, money, and suffering). Computer modelling of alternative control strategies, their effectiveness and likely consequences is a powerful tool and, as emphasised by Macdonald & Rushton (2003) confines at least some mistakes to virtual reality. In a related case, the eradication of the coypu from England, such simulations proved invaluable (Gosling & Baker 1987). Our team is currently working on an individual-based, spatial model of mink control, and an associated large-scale field experiment.

A holistic approach

Although new technology may change the situation, for the time being attempted control of American mink in Great Britain is likely to involve killing them. In some cases, this may suffice to protect native biodiversity—this is the optimistic suspicion for some upland areas in Scotland (e.g., Lambin et al. 1998). More generally, and particularly for the agricultural lowlands of England, we favour a more holistic approach, within which killing American mink is one component of an integrated package of measures. These measures should invariably include habitat restoration (to reverse the conditions of linearisation and fragmentation described by the tightrope hypothesis) and, due to the generally parlous state of the water vole, this species may often have to be re-introduced artificially (Macdonald et al. 2002c). However, exactly how killing American mink, restoring habitat, and nurturing water voles should be balanced in the mix will almost certainly vary with circumstances. It will depend on the geometry of local primary and secondary habitats and how they affect metapopulation functioning for each of the species involved (e.g., Bonesi et al. 2002). It will also depend on the balance of other species present: both prey and predator—most notably the otter and the polecat as members of the predator guild and the rabbit as their prey. If our predictions about intra-guild hostility are fulfilled—and the preliminary evidence is that they will be (L. Bonesi & D. W. Macdonald unpubl. data) then facilitating the recovery of otters (itself a priority of the United Kingdom Biodiversity Action Plan process) may be an important component of controlling American mink. In that case, it will be essential that models identify strategies where human interventions to remove mink work additively with the impact of competitors. These models must also take account of the pivotal importance of rabbits to American mink and, in turn, the influence of farming practice on rabbit distribution (Yamaguchi et al. 2003).

It is also important that strategies for attempted American mink control consider the criteria for identifying target areas. This is not only for reasons of efficiency and economy—with an eye to best biodiversity value—important as these drivers are. It is also because the killing of American mink is itself a cause of regret and, on principle, should be limited to what is necessary and effective. Of course, it should also be undertaken with regard to

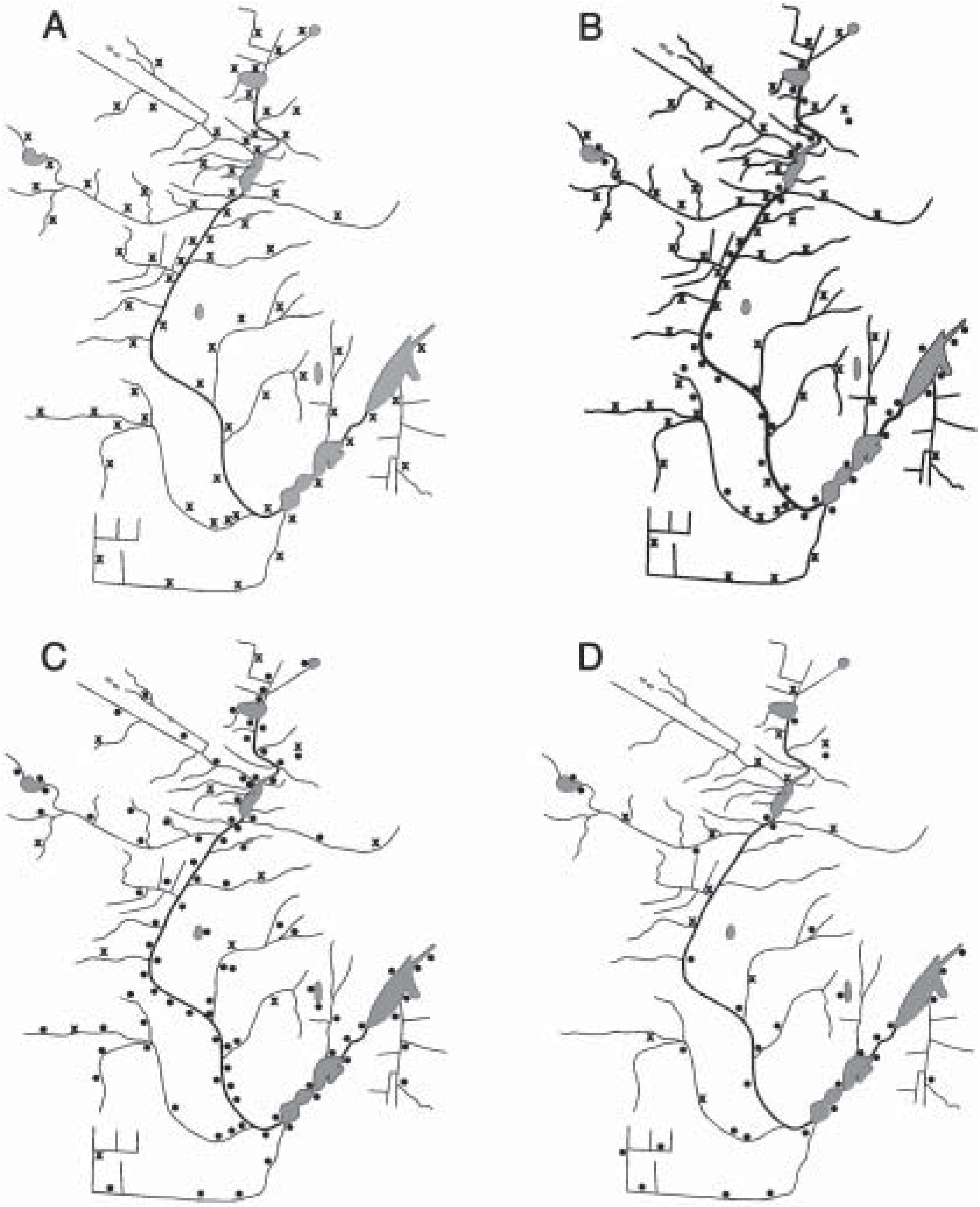


Fig. 8 Distribution of European (crosses) and American (circles) mink on the Lovat River, Belarus: **A**, before the expansion of the American mink (1986–89); **B**, at the beginning of the American mink's expansion (1990–91); **C**, when the American mink was at high density (1997–98); and **D**, after partial removal of the American mink (1998–99). Five European mink were also released in the area between 1998 and 2000. Reproduced from Macdonald et al. (2002).

humaneness. Indeed, Macdonald & Tattersall 2002 argue that the integration of animal welfare (and the science of measuring it) into wildlife conservation planning is likely to become a requirement.

So, to the tragedy and triumph of adaptation out of context. Thus far we have seen how people have transported the American mink far from its native range, and enabled us to witness the astonishing triumph of this beautiful species' marvellous adaptations over environments that span half the globe: a revealing, if unwitting and unhappy experiment in ecological theory. But the mink's triumph has brought tragedy almost wherever it has gone—in no cases more vividly than those of the water vole and the European mink, the two species on which our team has focused (Macdonald & Strachan 1999; Macdonald et al. 2002a).

This is not, however, the end of the story. Some of the damage done by introduced American mink may be reversible if conservationists intervene. For this intervention to succeed, and to be judged a success, we believe it will require inter-disciplinary work of the highest innovative calibre: it will embrace considerations of predator and prey biology, and habitat management, together with financial analyses and far-sighted policy. It will involve putting in the balance many factors that are weighed in incommensurable units. It will involve elegant modelling, ingenious fieldwork, and hard labour. If it works—that is, if native biodiversity is restored and enhanced—it will be another triumph. But that triumph, if it comes, will be bought at the cost of another tragedy—the deaths at human hands of many American mink. The cause of both these tragedies lies not with the American mink, or the marvel of their adaptability, but with the thoughtlessness with which people dispersed them.

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