BIODIVERSITY RESEARCH

Decline of invasive alien mink (*Mustela vison*) is concurrent with recovery of native otters (*Lutra lutra*)

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ABSTRACT

Invasive species often cause the decline of native prey or competitors. We highlight a contrasting example of the large-scale recovery of a native species and the concurrent decline and likely displacement of an established invasive competitor. Invasive American mink *Mustela vison* became widespread in the British Isles at the same time as native Eurasian otters *Lutra lutra* were declining as a result of water pollution. In common with other invasive predators, mink cause conservation problems for a range of native prey species, most notably water voles *Arvicola terrestris*. Recent trends in the distribution of native otters and invasive mink in north-east England were examined using a novel regression modelling approach to analyse presence/absence data from field surveys, corroborated by contemporary predator culling records. Between 1991 and 2002, the percentage of sites where mink signs were found decreased from 80% to 20%, while otter signs increased from 18% to 80%. Annual indices of mink captures on shooting estates increased between 1980 and 1996, but were followed by a decline thereafter. Indices of the incidence of native otters were significantly related to those indicating the decline or displacement of invasive mink. This large-scale field study is supportive of localized experimental evidence for the return of dominant, native otters being concurrent with the decline of the invasive alien mink. The recovery of a dominant native species may represent a reversal of the mesopredator release that allowed invasive mink to establish and may eventually serve to mitigate their impact on native prey species.

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INTRODUCTION

Invasive non-native species, particularly mammalian predators, are among the greatest threats to the conservation of biological diversity (King, 1984; Courchamp *et al.*, 2003). Such species may have deleterious impacts in a range of ways, including predation, competition for resources or by direct aggressive interactions with native species (Manchester & Bullock, 2000). Thus the impact of invasive species can be felt by both their prey and their competitors.

Among invasive mammalian carnivores, American mink *Mustela vison* Schreber have caused a variety of conservation problems as a result of their ability to establish over wide ranges and their effect on native prey, principally birds and small rodents (Banks *et al.*, 2004; Nordström & Korpimäki, 2004), and on competing species such as European mink *Mustela lutreola* L. (Sidorovich *et al.*, 1999; Lodé *et al.*, 2001). In the British Isles, where European mink were never present, American mink became widely established in the wild in the early 1960s, as a result of escapes and releases from fur farms (Thompson, 1962; Dunstone, 1993). It was initially suspected that feral mink would have a major impact on native wildlife, particularly game fisheries and waterbirds (Thompson, 1962; Lever, 1978; Linn & Chanin, 1978). In recent years, it has become clear that the establishment of mink in Britain has led to a marked decline in populations of ground-nesting birds (Craik, 1997; Ferreras & Macdonald, 1999) and water voles *Arvicola terrestris* L. (Woodroffe *et al.* 1990; Barreto *et al.* 1998; Macdonald & Strachan, 1999; Jefferies, 2003). The decline of water voles has been particularly steep, such that in the 1990s the English population declined by 80% (Macdonald & Strachan, 1999; Macdonald & Harrington, 2003).

During the period of the mink's establishment in the 1960s, there was a popular, scientific and, it later emerged, misplaced concern that mink may have had a role in the simultaneous decline in numbers and range of native Eurasian otters *Lutra lutra* L. (Lever, 1978; Linn & Chanin, 1978). Such an effect was felt most

likely to have arisen from competition for limited food supplies. However, studies of the diets of otters and mink in Britain and Ireland (reviewed by McDonald, 2002) have suggested that there is relatively little overlap in diet between the two species but that, in some areas where mink and otters coexist, mink change their diet in order to minimize competition (Erlinge, 1972; Chanin, 1981; Clode & Macdonald, 1995; Bonesi et al., 2004). Initial fears that competition with mink was harming the status of otters were unfounded and it has long been accepted that the otter's steep decline in Britain and elsewhere in western Europe during the latter half of the 20th century was caused largely by organochlorine pollution that peaked prior to the mink's arrival (Chanin & Jefferies, 1978; Jefferies, 1989).

While exploitation competition for food may not have been a major force in relations between invasive mink and native otters, an alternative mechanism affecting their status is interspecific aggression and/or intraguild predation. This process has recently been identified as commonplace in a range of taxa (Polis et al. 1989; Arim & Marquet, 2004), notably mammalian carnivores (Palomares & Caro, 1999). Wolves Canis lupus L. were recognized to have a major influence on coyotes Canis latrans Say, following wolf reintroduction to Yellowstone National Park (Crabtree & Sheldon, 1999; Switalski, 2003; White & Garrott, 2005). Among mesocarnivores, a major cause of mortality of red fox Vulpes vulpes L. and grey fox Urocyon cinereoargenteus Schreber is predation by sympatric coyotes or bobcats Lynx rufus Schreber (Gese et al., 1996; Fedriani et al., 2000; Farias et al., 2005). Complex interactions among predators can also lead to cascading trophic effects, such that when larger predators are removed from a system or reduced in abundance, perhaps by hunting or habitat fragmentation, the subsequent mesopredator release can effect substantial change in prey populations (Crooks & Soulé, 1999).

In most cases of interspecific conflict, body size is a predictor of the superior species (Palomares & Caro, 1999), and in the case of direct aggression between otters and mink, otters, which are approximately three times longer and 10 times heavier than mink (Corbet & Harris, 1991), might reasonably be expected to be the dominant species (Erlinge, 1972; Macdonald & Harrington, 2003). Nonetheless, evidence of direct aggression between otters and mink remains scarce. Grigor'ev & Egorov (1967) reported the occasional detection of mink remains in otter spraints. Novikov (1956) reported that otters 'vigorously hunt mink' in Russia. Erlinge (1972) identified reciprocal distribution of otters and mink in a Swedish lake system and observed that despite generally favourable conditions for mink, they disappeared seasonally and locally in response to the arrival of otters. Chanin (1981) supported Erlinge's (1972) suggestion, finding that despite the apparent lack of competition for prey, the presence of otters may have limited mink populations at Slapton Ley in England. Experimental support for the possibility of genuine interaction between the two species has recently been provided by local reintroductions of otters leading to rapid declines in feral mink populations in southern England (Bonesi & Macdonald, 2004a).

Otters received statutory protection in Britain in 1978 under the Conservation of Wild Creatures and Plants Act 1975, in 1982 under the Wildlife and Countryside Act 1981 and more recently under the EC Habitats Directive 1992. Because of this and various species recovery projects, otters are now increasing in number and range in Britain (Strachan & Jefferies, 1996; Crawford, 2003). We therefore wished to test the hypothesis, stemming from the proposition of competitive dominance made by Erlinge (1972), which was later echoed by Macdonald & Harrington (2003) and Bonesi et al. (2006), that the recovery of the native otter at a large scale may have precipitated the decline of the invasive mink at an equally large scale. The work of Bonesi & Macdonald (2004a) with reintroduced otters provides local, experimental support for the logic of this hypothesis. It is clearly not possible experimentally to test a hypothesis linking native and invasive species at a national scale. However, a testable prediction of this hypothesis is that, over time, indices of the status of each of these species based on field observations at a large scale should be negatively correlated to one another. Testing this prediction does not exclude other possible hypotheses for the decline of mink, but a failure to support this prediction would lead to the probable rejection of the hypothesis.

We investigated the changing status of invasive mink and native otters at a regional level, focusing on the north-east of England. Invading mink did not reach north-east England until the end of the 1960s (Johnston, 1974), after which the population grew in size and range through the 1970s and 1980s, although it remained at relatively low density compared to the rest of Britain (Strachan & Jefferies, 1996). Otters declined in north-east England, as they did in the rest of Britain at the same time that mink were arriving (Jefferies, 1989; Thom, 1997). If otters are now recovering in north-east England as they have done across the rest of the country (Strachan & Jefferies, 1996; Crawford, 2003) and if there are significant interspecific interactions between the two species, we predict that we will detect a contemporary decline in measures of mink incidence, which is likely to be related to declines in abundance and/or contraction in the species' range.

Field surveys of mink and otters benefit from corroboration by independent methods (Kruuk et al., 1986; Kruuk & Conroy, 1987; Bonesi & Macdonald, 2004b; Reynolds et al., 2004). Therefore, our long-term, extensive field surveys were accompanied by analysis of contemporary trapping records from gamekeepers that controlled for variation in trapping effort (McDonald & Harris, 1999; Davey & Aebischer, 2006).

METHODS

Field surveys of mink and otter presence were carried out at 195 sites on 12 river catchments (n sites per catchment 9–32) in north-east England (Fig. 1). Nine surveys were carried out annually in the winters between 1991 and 2002. No surveys took place in the winter of 2000/01 because of national access restrictions arising from outbreaks of foot and mouth disease. Surveys were conducted by trained volunteers and staff of the Northumberland Wildlife Trust following the protocols established by Britain's National Otter Survey (Strachan & Jefferies, 1996). Six hundred metres of one riverbank were surveyed around a central point and all footprints and mink scats and otter spraints were recorded.
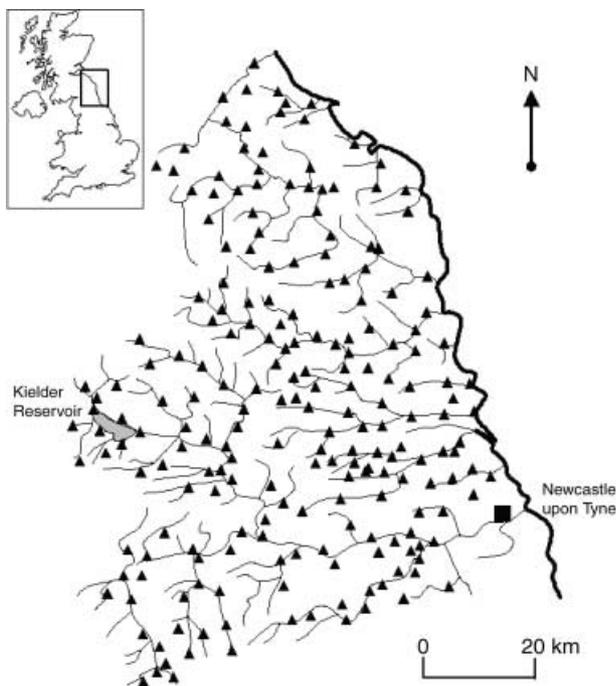
Figure 1 Otter and mink survey sites in north-east England.

Mink scats and otter spraints were distinguished on the basis of their distinctive morphology and odour (Strachan & Jefferies, 1996). Footprints were distinguished on the basis of their size. For a detailed account of the survey methodology and tests thereof, see Strachan & Jefferies (1996).

Analyses of trends in mink and otter incidence were based on the use of slopes from generalized linear models as indices of species status. This approach to analysing survey data has been successfully applied to birds, but is relatively novel for mammals and particularly novel for presence/absence data, so a brief account of the principles follows. In previous applications, a linear model, with an appropriate error structure (usually Poisson), is fitted to some measure of abundance, usually counts of a focal species, with spatial, temporal, habitat, anthropogenic, or other variables fitted as factors and/or covariates. Since the effects of these factors on counts can usually be described independently of one another, they provide a means of isolating main effects such as trends in time, that are then independent of confounding factors such as regional variation, missing values, or sampling effort (van Strien *et al.*, 2004). This approach is particularly suitable for developing large-scale indices of status and has been adopted for the analysis of large and complex data sets from bird surveys (van Strien *et al.*, 2001, 2004; Gregory *et al.*, 2005) and more generally for the inference of time series trends (TRIM, TRends and Indices for Monitoring data, Pannekoek & van Strien, 2001). In this instance, however, the response variable is not direct counts of animals, but the presence or absence of mink and otters at each of the survey sites. Therefore, a logistic regression approach was adopted rather than a Poisson regression. Otherwise, this approach to analysis of mammal survey data is similar to that adopted by Gregory *et al.*

(2005) for birds. Specifically, dealing with each river catchment separately, a logistic regression model was fitted to mink presence and absence with survey site ($n = 9–32$ per catchment) and survey ($n = 9$) as factors. As with Gregory *et al.* (2005), the slopes (or coefficients, usually denoted as β in model outputs) from each level of the factor, survey year, were calculated by corner-point parameterization, and these parameter estimates were taken as an annual index of mink presence for each catchment, relative to the first survey year and independent of within-catchment, among-site variation (van Strien *et al.*, 2001). The same analysis was repeated for the otter survey data to derive indices of otter presence.

Once these indices were calculated, a more straightforward analysis was conducted. Factors affecting the indices of mink and otter presence were then analysed by fitting a linear model to the annual indices for each species, with river catchment as a factor and survey year now fitted as a continuous variable. A survey year*catchment interaction term was included but subsequently omitted if found to be non-significant. At this stage, cases were weighted by 1/variance of the annual index.

Finally, annual indices of mink presence for each catchment and survey year were regressed against the matched indices of otter presence; cases were again weighted by 1/variance of the mink and otter slopes. This analysis has the advantage that it capitalizes on the fact that the magnitude of change in otter and mink status is preserved by the indices developed above, i.e. this regression tests the assertion that when and where otter recovery is most pronounced, the change in mink status is also most pronounced. A more conventional analysis of species presence or absence (Erlinge, 1972) would only be able to associate the absolute presence or absence of one species to the other. Our approach could therefore be construed as akin to a natural experiment where the magnitude of treatment (otter recovery) is varied and the response (mink index) measured.

A corroborative source of data was used to verify the results of extensive field surveys of mink only. Trapping records (bags) for mink were obtained from all the shooting estates in the north-east region of England that participated in the National Gamebag Census (NGC) between 1980 and 2001. The NGC is a long-term survey of the shooting and trapping records of sporting estates collated by The Game Conservancy Trust (Tapper, 1992). Trends in the total numbers of mink that were caught on single estates using cage traps, spring traps, and by shooting were investigated by a similar method as above. A regression model was fitted to the $\log_{10}$-transformed mink bag with estate and year as factors and the number of gamekeepers working on the estate as a covariate measure of trapping effort (McDonald & Harris, 1999). Year coefficients can then be taken as annual indices of mink bag relative to the first year of the census data that are independent of among-estate variation and variation in the number of gamekeepers participating.

RESULTS

Between 1991 and 2002 the number of sites where mink signs were found decreased from 80% to 20%, while otter signs
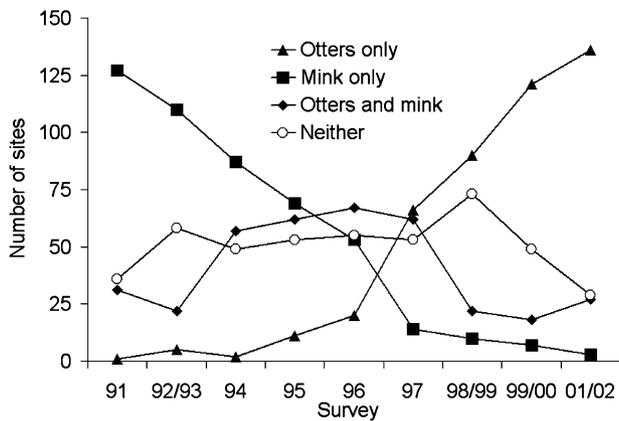
Figure 2 Trends in site occupancy by otters and mink between 1991 and 2002. The number of sites surveyed in each year was 195. Note that the total number of sites occupied by mink is the sum of the sites occupied by mink alone and sites occupied by both mink and otters.

increased from 18% to 80% (Fig. 2). The number of sites where both species were present increased in the initial phase of the survey but was then followed by a decline. The number of sites where neither species was found remained approximately stable throughout the survey.

Annual indices of mink presence were not significantly affected by the survey year*catchment interaction term and so the model was refitted with no interaction term. There was a significant decline in annual indices of mink presence with survey year (slope = −0.805, $F_{1,83}$ = 290.3, P < 0.001) but indices did not vary significantly among catchments ($F_{11,83}$ = 0.033, P > 0.9). Annual indices of otter presence were significantly affected by variation in the survey year*catchment interaction term ($F_{11,72}$ = 4.67, P < 0.001), among catchments ($F_{11,72}$ = 3.56, P < 0.001) but not with survey year ($F_{1,72}$ = 0.139, P = 0.711). Annual mink indices were significantly and negatively related to annual otter indices (Fig. 3: r^2 = 0.169, slope = −0.1, $F_{1,94}$ = 19.13, P < 0.001).
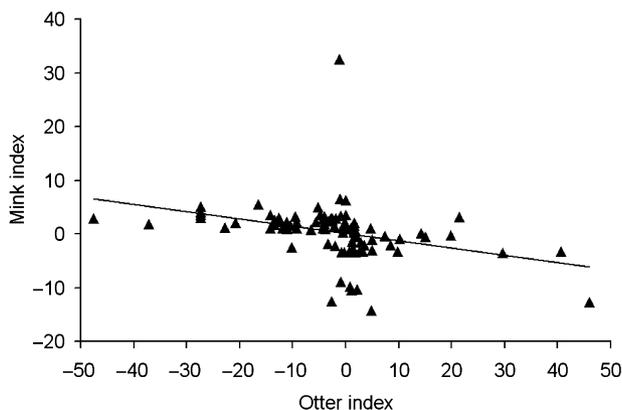

Figure 3 Relationship between otter presence and mink presence. Each dot represents the index of mink and otter presence on one river catchment in one survey.
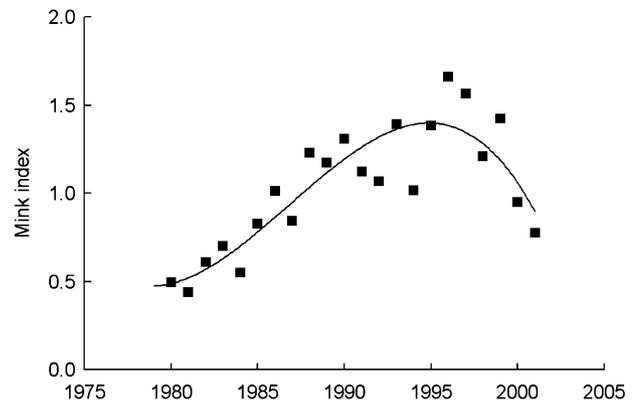

Figure 4 Trend in index of mink trapping records from 17 shooting estates in north-east England, 1980–2001.

Annual indices of the numbers of mink trapped on shooting estates, which are independent of among-estate variation, indicated an increase in mink bags between 1980 and 1996 followed by a steep decline thereafter. The best fit to these data was obtained by fitting a third-order polynomial curve (r^2 = 0.84, P < 0.001), the turning point of which was in late 1994 (Fig. 4).

DISCUSSION

We detected a statistically significant relationship between the decline in incidence of an invasive mammal between 1991 and 2002 and the simultaneous recovery of a native competitor, the rate of which varied among river catchments. Trends in mink incidence from field surveys were corroborated by the independent trapping data from local game estates.

In the early 1990s, three trends were apparent (Fig. 2): (1) the number of sites where signs of invasive mink were found and no otter signs were found was decreasing; (2) the number of sites where signs of both native otters and invasive mink were found was increasing; and (3) the number of sites where only signs of otters were found or neither species was present remained stable or increased slowly. From the mid-1990s onwards: (1) the number of sites where mink were detected either with or without otters declined markedly and (2) the number of sites where only otters were detected increased markedly. For mink, this pattern was matched by the observed decline in the numbers trapped by gamekeepers in the same region in the mid-1990s. These trends suggest that during the 1990s, native otters expanded their range by reoccupying areas where mink were living and that mink were subsequently not detected at these sites. In their recent extensive survey, Strachan & Jefferies (1996) noted that where otters had reached high densities, mink tended to be eliminated and that 'empty' sites were only rarely colonized by either species.

The statistically significant relationship between the changing incidence of signs of invasive mink and native otters is suggestive of a link between the recovery of the native and the decline, or at best the spatial displacement, of the invasive species. Experimental support for the possibility of genuine decline has recently been provided by local reintroductions of otters leading to rapid

declines in feral mink populations in southern England (Bonesi & Macdonald, 2004a). Field surveys detail the incidence of conspicuous signs and clearly cannot prove absence where signs are not detected. For this reason, the corroborative patterns shown by trapping record data are particularly helpful. While trapping records are subject to bias, variation in trapping effort has been controlled for (McDonald & Harris, 1999) and they can provide an index of presence, range, and abundance that is not reliant on detecting signs (Davey & Aebischer, 2006). Nonetheless, while these field observations are compelling, it should be remembered that our extensive survey data and corroborative trapping data demonstrate the pattern and not necessarily the cause.

What might be the mechanism by which otters may be affecting mink? Previous studies of otter–mink interactions have focused on dietary competition, though we believe this to be an unlikely cause of the decline of mink for two reasons. First, the diets of the two species do not overlap greatly in most habitats (Wise *et al.* 1981; Clode & Macdonald, 1995; McDonald, 2002). In most habitats, otters are predominantly piscivorous, whereas mink diet is dominated by mammalian prey (Akande, 1972; Dunstone & Birks, 1987; Dunstone, 1993; McDonald, 2002). Second, this dietary difference is accentuated where the two species live in sympatry such that where they do coexist, mink are more generalist predators, taking a high proportion of mammalian prey (Gerell, 1967; Erlinge, 1972; Chanin & Linn, 1980; Clode & Macdonald, 1995).

Direct aggression between otters and mink seems a plausible mechanism for the decline of mink. Intraguild predation and interspecific killing are recognized as widespread, particularly among mammalian carnivores (Palomares & Caro, 1999). Aggression between North American mink and Eurasian otters has not been studied in depth but has been reported to a limited degree in the literature (Dunstone, 1993). It has also been indirectly inferred from the avoidance by mink of areas inhabited by otters (Erlinge, 1972). Direct aggression has been suggested as the mechanism by which invasive American mink have caused a decline in smaller European mink in eastern Europe (Maran *et al.*, 1998; Sidorovich *et al.*, 1998). Nonetheless, Melquist *et al.* (1981), working in the American mink's native range in Idaho, found that mink and river otter *Lontra canadensis* Schreber often chose dens near one another and rarely interacted aggressively despite competition for food resources and feeding sites. Similarly, Ben-David *et al.* (1995) provided evidence of niche separation between the American mink and river otters but could not link it to competition. Antagonistic interactions between American mink and Eurasian otters may have a more pronounced effect in Britain because, unlike American mink and river otters, they have not had sufficient time to reach a state of 'equilibrium' (Strachan & Jefferies, 1996), though rapid responses in dietary composition and habitat segregation have been identified in sympatric mink and otter populations in southern Britain (Bonesi & Macdonald, 2004c; Bonesi *et al.*, 2004).

We conclude that the indisputable recovery of native otters has been concurrent with and may have had a role in the apparent decline of invasive mink. Since otters present little or no threat to the native mammals or birds eaten by mink, otter recovery programmes may be beneficial for the additional reason that otters may facilitate the persistence of species, such as water voles, for which the presence of mink is detrimental (Bonesi *et al.*, 2006). While declines in invasive species due to 'ecological overshoot' or senescence of the population have been documented (King, 1984; Cronk & Fuller, 1995; MacNeil *et al.*, 2003), the pattern of recovery of a native predator concurrent with the decline of its invasive competitor has few precedents. It is in marked contrast to the grave and ongoing impacts of invaders in regions where dominant native species are scarce or absent, due to unrelated conservation problems. The role of recovered populations of native predators in mitigating the impact of invasive species holds significant promise as an unexpected solution to the ecologically and economically costly problems of alien invasions.

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