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Original Investigation

A foe in woe: American mink (*Neovison vison*) diet changes during a population decrease

Rannveig Magnusdottir[a,b,c,*], Menja von Schmalensee[a,b], Robert A. Stefansson[a,b], David W. Macdonald[c], Pall Hersteinsson[a]

[a] Faculty of Life and Environmental Sciences, University of Iceland, 101 Reykjavik, Iceland
[b] West-Iceland Centre of Natural History, 340 Stykkisholmur, Iceland
[c] Wildlife Conservation Research Unit, Zoology Department, University of Oxford, The Recanati-Kaplan Centre, Tubney House, Tubney, Oxford OX13 5QL, UK

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ABSTRACT

The invasive American mink has been a component of Iceland's fauna since the 1930s. Hunting statistics indicate that until 2003 the population size was increasing, but thereafter decreased rapidly. The Icelandic marine environment has experienced various changes in recent years, including rising sea temperature and sand-eel collapse followed by seabird recruitment failure and population declines. Furthermore the arctic fox population has increased at least six-fold in the last three decades. Mink stomach content analysis in the period 2001–2009 revealed diet changes, and signs of reduced prey availability for this generalist predator, that were most significant in males. The most marked shift in composition was a decrease in consumption of birds. Our findings suggest that climate events, together with competition with increasing numbers of arctic foxes over terrestrial food, contributed to the sharp reduction in the mink population from 2004 and onwards. Despite their generalist behaviour, mink have apparently failed to respond fully to these environmental changes, and this susceptibility may benefit attempts to control their numbers. The results are relevant to the ability of top predators in general to cope with diverse ecosystem alterations triggered by climate change.

Introduction

The American mink *Neovison vison* is a widespread, opportunistic and generalist carnivore that is ranked among the 100 most invasive species and one of the four most invasive mammals in Europe (Nentwig et al., 2010; DAISIE, 2011). The mink was first brought to Iceland in 1931 for fur farming and, following escapes, had colonised the entire coastal lowland by 1975 (Skirnisson and Petersen, 1980). In an attempt to minimise damage by mink to the native fauna, it has been hunted extensively and, since 1939, under bounty. In Iceland, mink diet is very diverse for both sexes but females eat more fish and fewer birds than do males and sex-related dietary differences of mink is greater in coastal habitats. These differences are probably driven by sexual dimorphism in body size of mink and the variability of available prey types available. In habitats with high variability of prey types, such as many coastal areas, the sexes are able to hunt different prey species, while in habitats with low variability in prey types, such as many riparian areas, the sexes are forced to utilise a similar composition of prey (Magnusdottir et al., 2012). Mink feeding habits may be an indicator of relative prey abundance (Dunstone, 1993).

Little is known about the mink's impact on the native Icelandic fauna but some bird species are thought to have been negatively affected, e.g. the water rail *Rallus aquaticus*, horned grebe *Podiceps auritus* and black guillemot *Cepphus grylle* (von Schmalensee, 2010). In addition to a possible negative effect on natural bird and fish populations, the presence of mink in eider *Somateria mollissima* colonies can have detrimental financial consequences for farmers harvesting the down. The number of mink killed annually in Iceland increased steadily, with some fluctuations, from the 1930s until 2003. Until the 1980s, this increase largely reflected the range expansion within Iceland. Since 2004 the annual tally countrywide has plummeted, despite little change in hunting efforts, and in 2010 the number had dropped to almost half of its value in 2003 (Fig. 1). A mark-recapture study conducted in the Snaefellsnes Peninsula, West Iceland, indicated a considerable reduction in mink density between 2002 and 2006 (Hersteinsson et al., 2012).

Globally, a broad range of organisms has been affected by recent climate changes (Ottersen et al., 2001; Stenseth and Mysterud, 2002; Stenseth et al., 2002; Walther et al., 2002; Root et al., 2006; Hatun et al., 2009). There are indications of rapid changes in the marine environment, e.g. in the North Atlantic Ocean where temperature has increased, affecting the availability of planktonic food

* Corresponding author at: Faculty of Life and Environmental Sciences, University of Iceland, 101 Reykjavik, Iceland. Tel.: +354 8650065; fax: +354 525 4069.
E-mail address: rannveigm@gmail.com (R. Magnusdottir).

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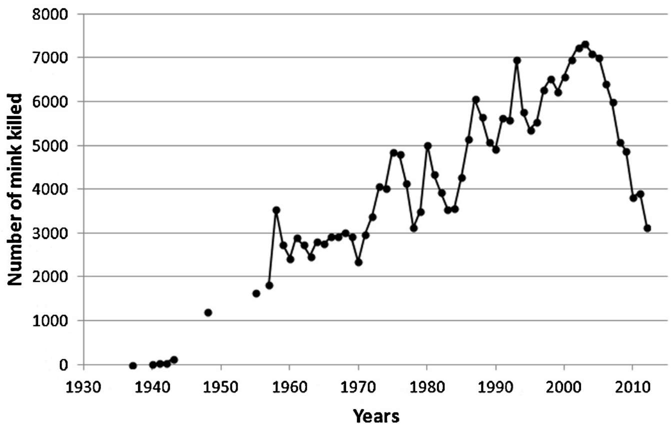

Fig. 1. The annual number of mink killed in Iceland in 1937–2012.

for fish larvae, which determines the sizes of many fish populations (Walther et al., 2002). The collapse of key-stone species can put whole ecosystems in peril. An example is the sand-eel (*Ammodytes marinus*) in the North Sea, which is depended upon by other fish and numerous seabird species and has experienced severe dynamic downswings (Arnott and Ruxton, 2002). The sand-eel population in Iceland has been decreasing for more than a decade and suffered from a severe recruitment failure in 2005 and 2006 (Bogason and Lilliendahl, 2009). As a result, numerous seabirds that depend on the sand-eel for food during the breeding season, have also been declining (Gardarsson, 2006; Thrainsson et al., 2011).

The arctic fox (*Vulpes lagopus*) is the only native terrestrial mammal in Iceland and the only other mammalian carnivore besides the mink. Both mink and arctic fox in Iceland have very varied diets and although the diet of these two sympatric carnivores does not overlap extensively, they both prey on birds. Overlap seems to be highest for fulmar *Fulmarus glacialis*, ducks and waders (Hersteinsson and Macdonald, 1996; Magnusdottir et al., 2012). A recent study in Sweden showed that the population dynamics of red fox *Vulpes vulpes*, due to changes in prey abundance, caused fluctuations in mink populations (Carlsson et al., 2010). Yet to date there is no direct evidence of arctic foxes impacting mink population size in Iceland. In contrast to the mink population in Iceland that started decreasing in 2004 after doubling in numbers from the late 1970s (Hersteinsson et al., 2012), the arctic fox population has increased at least six-fold since the late 1970s and an overall rise in food abundance is thought to be the main factor responsible (Hersteinsson et al., 2009). This overall rise is partially due to natural circumstances but most likely also driven by human activity, such as an increase in use of unsupervised fox bait by hunters in winter.

In this study we used mink stomach contents to examine if, and to what extent, mink diet has changed in the last decade, and whether this reflects changes in the marine- and terrestrial environment in Iceland. We predicted that as the population size changed during the years 2001–2009, there were significant changes in the mink's prey, and that these changes might differ between males and females.

Material and methods

Study area

The study was conducted in and around the Snaefellsnes Peninsula in West Iceland and comprised Snaefellsnessysla county as well as small islands and coastal areas in the mouth of the fjord Hvammsfjordur, Dalasysla county, approx. 64.42–65.18°N,

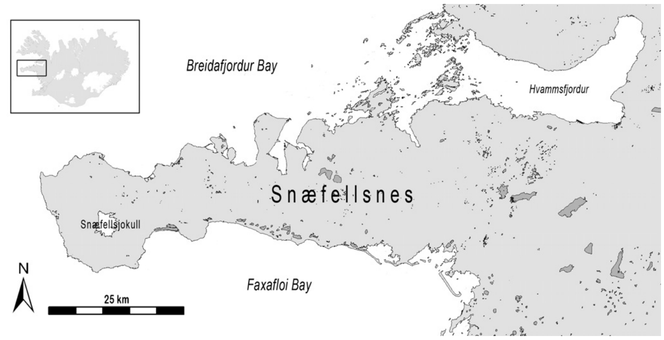

Fig. 2. The study area in the Snaefellsnes Peninsula, West Iceland. Dark grey areas indicate freshwater lakes.

21.37–24.02°W (Fig. 2). The Snaefellsnes peninsula predominantly consists of a mountain ridge with the Snaefellsjokull glacier (1446 m) at its western tip. The coastline of the study area is approximately 600 km (excluding islands) and the area is roughly 1300 km^2 with 740 km^2 within 0–200 m above sea level. These lowland coastal, semi-coastal and freshwater areas provide both diverse and suitable habitats for mink, while the mountainous ranges appear not to be used by them on a regular basis. The annual average air temperature in Stykkisholmur on the Snaefellsnes Peninsula, increased significantly (Pearson $P = 0.028$) from 3.8 °C in 1999 to 4.7 °C in 2009, while there was no significant trend in average coastal sea temperature around Iceland in that time period (data obtained from the Icelandic Met Office and the Icelandic Marine Research Institute).

Stomach sample collection and data division

In total, 662 mink carcasses (357 males and 305 females) obtained from mink hunters in the years 2001–2009 were studied. All animals were either shot or instantly killed with non-baited lethal traps, and the hunting methods did not change between years in the study period. The hunting technique therefore did not influence stomach contents. Empty stomachs were included in all analyses since they were thought to reflect real changes in the environment. Thawed stomachs were weighed, bones, feathers, hairs, otoliths, exoskeletons of arthropods and other identifiable prey remains from mink stomachs were examined thoroughly (i.e. frequency of occurrence and prey weight) and remains were classified to order or species level if possible, as explained further in Magnusdottir et al. (2012).

Each prey species, or a prey group, was analysed separately for males and females and compared between years in three ways: (1) whole years (starting in September and ending in August the subsequent year), (2) warm season (April–August) and cold season (September–March) and (3) each of the four seasons: spring (April–May), summer (June–August), autumn (September–November) and winter (December–March). First, statistical analysis was performed on individual fish species, but since this revealed no significant species-based differences in diet between years, fish were thereafter combined into two groups: marine and freshwater fish, although the unidentified group of fish was sometimes large. All fish species were also analysed together (henceforth termed 'all fish'). Similarly, statistical analysis was performed on birds on the lowest taxonomic level possible in addition to birds divided into three groups: seabirds, ducks and "other birds" (mostly waders). Furthermore, birds were also analysed as a single group (henceforth termed 'all birds'). It was not possible to categorise bird species into marine and freshwater birds since many species use both habitats. Invertebrates were analysed as four groups: crustaceans (Crustacea), insects and arachnids

(Insecta and Arachnida), starfish (Asteroidea) and all invertebrates together in one category termed "all invertebrates". The category "all invertebrates" was used in the presentation of the results due to lack of significance in analyses of the 3 component categories and the term "other" prey indicates both wood mice *Apodemus sylvaticus* and invertebrates. The term "multiple prey" refers to cases where two or more prey types were found in the stomach sample, for example both fish and bird, or fish, mouse and insect. "Multiple prey" is a separate category used to illustrate temporal changes in the number of prey types consumed within the last day. Each individual mink was classified according to the location of capture as either riparian (in riparian areas and/or >1 km from the coast) or coastal (in coastal areas, which in some cases contained stretches of freshwater rivers). The time period 2001–2009 was analysed both as a series of individual years and, due to possible differences during population increase and population decrease, divided into two time periods 2001–5 (300 mink between autumn 2001 until summer 2005) and 2005–9 (362 mink between autumn 2005 until summer 2009) which were compared for all seasons and habitats. When direct comparisons of the sexes were made, the weight of the stomach contents was standardised (using average weight of stomach content $\times$100/average weight of all same sex animals), since male mink are much larger than females.

Statistical analyses

Food consumption in relation to year, habitat, season and sex was compared for (1) % mass using Kruskal–Wallis non-parametric one way analysis of variance, Dunn's post hoc test for multiple comparisons and Mann–Whitney *U* test and (2) for frequency of occurrence using Fisher's exact test and Chi square test of independence. The overall sample size was usually very good, but groups containing less than 10 individuals were omitted from further analyses. The statistical program used was GraphPad Prism version 5.0 for Windows, GraphPad Software, La Jolla, California, USA. Mink prey type and multiple prey trends in diet were calculated using logistic regression in the statistical program SPSS for Windows, version 14, SPSS Inc., Chicago, USA.

Results

Prey remains were found in 490 out of 662 stomachs collected in the period 2001–2009. Of 305 stomachs from females, 243 (80%) contained prey remains, whereas for males 247 out of 357 (69%) contained prey remains. Males had significantly more empty stomachs than females did (Fisher's exact test, $P = 0.0025$). Stomach contents were very diverse and consisted of various fish, bird and invertebrate species in addition to wood mouse. Fish species identified were both marine fish (bull rout *Myoxocephalus scorpius*, lumpsucker *Cyclopterus lumpus*, butterfish *Pholis gunnellus*, fivebeard rockling *Ciliata mustela*, pollock *Pollachius virens*, sand eel *Ammodytes* spp. and Gadiformes spp.) and freshwater fish (*Salmonidae* spp. and three-spined sticklebacks *Gasterosteus aculeatus*). Bird species identified were seabirds (mostly fulmar but also alcids, *Alcidae* spp., and gulls, suborder Lari), ducks (Anseriformes) and "other birds" (Charadriidae, Scolopacidae and Passeriformes) (Appendices 1 and 2). Most of the ducks may have been eider since they are by far the most abundant duck in Iceland (Asbirk et al., 1997; Gardarsson, 2009). Egg consumption was recorded in both sexes all year round.

Stomach content weight

For males, the average weight of all stomach contents during the time period decreased significantly (Spearman test; $P = 0.0091$) and stomach contents were significantly heavier in 2001–5 than in 2005–9 (Mann–Whitney test; $P = 0.0035$) and significantly heavier in 2004–5 than in 2008–9 (Kruskal–Wallis: $P = 0.013$, Dunn's post test: $P < 0.05$). For females, the average weight of all stomach contents during the time period did not change significantly, although some fluctuations occurred and the weight neither differed significantly between years nor between the two time periods 2001–5 and 2005–9.

For both sexes, the weight of stomach contents was stable and proportionally similar relative to their body weights from 2001 to 2004 (Fig. 3). For males the weight peaked in the warm season of 2005 but crashed in the cold season of 2005–6; trends were similar, but less marked, for females. Thereafter, for both sexes, the weight fluctuated.

Diet changes

Overall, changes in diet were observed in both sexes in both habitats. While the average weights of the predominant categories of prey (fish, birds and other) were quite stable throughout the study period for females, males experienced large fluctuations (Fig. 4).

Fish: Whereas there were no significant trends in the years 2001–2009 in the consumption of freshwater fish or marine fish by either sex (logistic regression analysis), there was a significant increasing trend in the consumption of all fish by females and both sexes combined in spring (Table 1). Proportionally, females consumed significantly more marine fish than did males (Mann–Whitney test; $P = 0.013$, Fisher exact test; $P < 0.0001$) and the majority of fish consumed by males was of freshwater origin. Combined fish consumption of males was extremely little in the years 2005–6 and 2008–9 and the data indicate that they consumed more fish in the first half (2001–2005) of the study period compared to the latter half (2005–2009) (Fig. 4B), although this trend was not significant due to large variation. There were no significant changes in average annual consumption (weight) of marine fish, or all fish combined by either sex of mink, although for females, freshwater fish was highest in summer diet of 2004 but decreased after that.

Birds and mammals: Logistic regression revealed a general decline in frequency of bird consumption (all birds, seabirds, ducks and waders; Table 1 and Appendices 3 and 4), although males' diet explained most of the decline. Coastal males (in all seasons combined) consumed less seabirds in 2005–9 than in 2001–5 (Mann–Whitney test; $P = 0.041$; Appendix 5). Test statistics for individual years and the two time periods (Table 2 and details in Appendices 5–7), corroborated the decreasing numbers and quantity of birds (ducks, waders and all birds combined) in mink diet, and revealed some other differences between years, e.g. that wood mouse consumption peaked in male mink diet in the years 2003–4 and 2008–9 (Table 2).

Invertebrates: Invertebrate consumption increased throughout the time period in both sexes, and a steady increase in multiple prey consumption in males coincided with the increased frequency of invertebrate intake (Tables 1 and 2 and Appendices 3–7). Some males consumed large quantities of starfish (Asteroidea) in the cold months of 2004–5, 2005–6 and 2006–7, although the difference between years was not statistically significant.

Discussion

Management of well-established alien invasive species, like the mink, is more likely to succeed when the population biology of the species is well known (Macdonald et al., 2002; Simberloff, 2003; King and Strachan, 2006). In planning population reduction of invasive species, it is important to know which elements of their ecology most stringently limit their numbers. This study

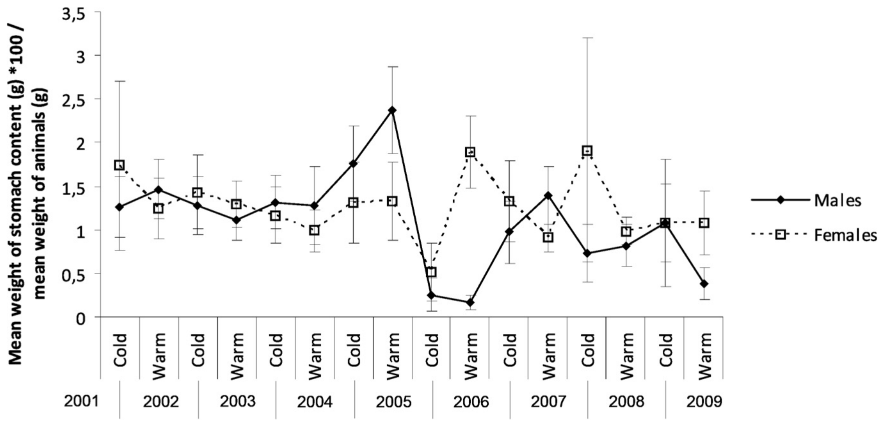

Fig. 3. Standardised weight of stomach content for all males and females in the cold and warm months of the years 2001–2009 (Average weight of stomach content (g) ×100/average weight of animals (g)). In the warm season of 2006 and the cold season of 2007–8 females had proportionally higher average weight of stomach contents than did males (*t*-test. $P=0.0085$ and $P=0.001$, respectively).

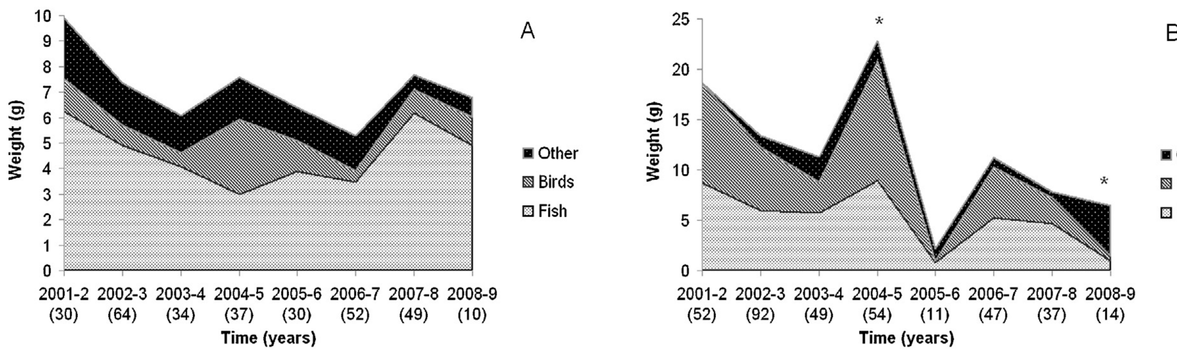

Fig. 4. Average weight of fish, birds and other food (wood mice and invertebrates) in stomach content of (A) females and (B) males. The numbers of samples per year are indicated below the years. Stars indicate a significant difference in total weight between years.

encompassed years during which the mink population in Iceland increased, peaked and entered a downswing, and is the first study to analyse temporal trends in a mustelid's diet. Significant changes were observed in mink diet during the years 2001–9 and while changes were noted in all seasons, they were most significant in spring and summer when samples were largest and when migrating birds were an important prey group in mink diet, especially for males. The most marked change in diet was a decline in the consumption of birds. The reduction in weight of stomach contents in the latter half of the study period, especially in males, indicates that mink in Iceland probably experienced food shortage and our results suggest that the decline in the mink population is likely to be associated with changes in its food availability. In Iceland, male mink consume more birds and less fish than do females, which may be explained by their smaller body size and possible limitation in catching larger birds (Magnusdottir et al., 2012). This, in the context of a decline in bird prey in mink diet, may explain why males experienced greater diet changes than did females. This accords with our prediction that diet changes would differ between the sexes and, since males are larger and require more energy than females, it is likely they are more affected by food shortage than are females. We considered three non-exclusive, possible explanations for mink diet changes: (1) decline in prey populations, (2) less access to prey and (3) impaired hunting ability.

Table 1
Logistic regression of mink prey type trends in the years 2001–2009 in the whole Snaefellsnes Peninsula. Trend is classified as % decrease/increase (arrows) per year.

	All seasons	Spring	Summer
Both sexes	$n=662$	$n=318$	$n=77$
All fish	–	23% ↑ ($P=0.003$) $n=165$	–
All birds	11% ↓ ($P=0.011$) $n=165$	25% ↓ ($P<0.0005$) $n=72$	–
Seabirds	20% ↓ ($P=0.046$) $n=23$	–	–
Ducks	14% ↓ ($P=0.042$) $n=52$	–	27% ↓ ($P=0.025$) $n=12$
Waders	–	37% ↓ ($P=0.002$) $n=20$	–
Invertebrates	17% ↑ ($P<0.0005$) $n=173$	–	–
Multiple prey	9% ↑ ($P=0.049$) $n=170$	–	–
Males	$n=357$	$n=160$	$n=31$
Ducks	17% ↓ ($P=0.046$) $n=37$	–	–
Invertebrates	26% ↑ ($P=0.001$) $n=74$	29% ↑ ($P=0.009$) $n=35$	–
Multiple prey	14% ↑ ($P=0.049$) $n=81$	–	–
Females	$n=305$	$n=158$	$n=46$
All fish	–	23% ↑ ($P=0.041$) $n=98$	–

Table 2
Test statistics, where significant, for interannual variation in diet of mink in the years 2001–2009 as well as for changes in mink diet between the years 2001–2005 and 2005–2009. Significant differences in prey frequency (Fisher exact and Chi square test) and weight (Kruskal–Wallis (KW), Dunn's post tests and Mann–Whitney (MW) test) in diet of mink in different seasons. Arrows next to years represent high consumption (↑) and low consumption (↓) of prey involved.

	Prey species	Season	Frequency of occurrence	Variation	%mass	Variation
Males	Ducks	Summer	–	–	KW: $P = 0.013$	Dunn's: 2003–4↑, 2006–7↓, 2007–8↓
	Ducks	Summer	Fisher: $P = 0.0026$	2001–5↑	–	–
	Wood mouse	All	Chi: $P = 0.0091$, df = 6	2001–2↓, 2002, 3↓, 2003–4↑, 2007–8↓, 2008–9↑	–	–
	Invertebrates	All	Chi: $P = 0.0038$, df = 6	2001–2↓, 2002–3↓, 2004–5↑, 2006–7↑, 2007–8↑, 2008–9↑	–	–
	Invertebrates	All	Fisher: $P = 0.023$	2005–9↑	–	–
	Invertebrates	Summer	Fisher: $P = 0.046$	2005–9↑	–	–
Females	All fish	Spring	Chi: $P = 0.03$, df = 7	Lowest in 2002, highest in 2007	–	–
	Freshw. fish	Summer	–	–	KW: $P = 0.0029$	Dunn's: 2004↑, 2005↓, 2007↓, 2008↓
	All birds	Spring	Chi: $P = 0.0032$, df = 7	2002↑, 2003↑, 2004↑, no birds in 2007, 2008	KW: $P = 0.0026$	Dunn's: 2002↑, 2004↑, 2007↓, 2008↓
	All birds	Spring	Fisher: $P = 0.0026$	2001–5↑	MW: $P = 0.0064$	2001–5↑, 2005–9↓
	Ducks	Spring	Chi: $P = 0.0034$, df = 6	2003↓, 2004↑	KW: $P = 0.018$	Dunn's: not significant
	Waders	Spring	–	–	MW: $P = 0.042$	2001–5↑, 2005–9↓
	Invertebrates	Summer	–	–	KW: $P = 0.008$	Dunn's: 2002↓, 2006↓, 2008↑
	Invertebrates	All	Fisher: $P = 0.0038$	2005–9↑	–	–
	Invertebrates	Autumn	–	–	MW: $P = 0.048$	2001–5↓, 2005–9↑

Decline in prey populations

In Iceland, little is known about many of the mink's main prey species. Freshwater fish, mostly salmonid parr, decreased, albeit not significantly, in mink diet through the study period, but simultaneously increased in rivers (Institute of Freshwater Fisheries).

Most marine species eaten by mink are not utilised by man and little is known of their availability. A higher proportion of bull rout remains were found in Icelandic coastal mink diet in 1978–79 (Skirnisson, 1979) than in 1997–2009 (Magnusdottir et al., 2012), which might indicate a decline in the bull rout population, but the two studies were conducted in different areas. Temperatures in southwest Iceland, in both winter and summer, have generally increased over the past 30 years. There was a dramatic recruitment failure and population decrease of various fish and seabird species in Iceland around the year 2005, indicating drastic and ongoing changes in the marine environment. This coincides with the decreasing trend in seabirds (mostly fulmars) in mink diet. Seabirds are however a fairly small portion of mink's diet in Iceland (Magnusdottir et al., 2012), but their decline may reflect change throughout the marine food chain that affected the availability of mink prey more generally. Little is known about the population dynamics of most waders and ducks in Iceland, except that the common eider population has decreased since the 1990s (Jonsson et al., 2013), which mirrors the decrease in ducks in mink's diet. However, some bird species which are preyed upon by foxes but not by mink, are increasing in numbers in Iceland, e.g. graylag geese *Anser anser* and pink footed geese *A. brachyrhyncus*, possibly due to improved conditions in the wintering grounds (Hersteinsson et al., 2009 and references therein).

Trends in mink diet probably offer, in general, a proxy for estimating the relative availability of various species, as seen with the coincidence between increasing wood mouse populations in 2003 (Unnsteinsdottir and Hersteinsson, 2009) and wood mouse consumption by mink. Overall, the reduced stomach contents in males, and the overall increase in multiple prey and consumption of less nutritious invertebrate prey, such as the substantial starfish consumption by some male mink in the cold months of 2004–2007, indicate that mink were increasingly facing different sorts of shortages during the study period.

Available data indicate that the population size of different mink prey species either decreased or increased respectively in the study period but in many cases data thereon are not available and not all mink diet changes in the study period can be explained by a decline in prey population sizes.

Less access to prey

Mink can lose access to prey due to competition or changes in prey behaviour. There has been little evidence of direct competition between mink and arctic foxes, although the foxes sometimes disturb foraging mink and steal their prey (Hersteinsson, 1984). It has not been thought likely that foxes are important predators of mink in Iceland and mink remains are hardly found at arctic fox dens and not found in fox stomachs (Helgason, pers. comm.; Hersteinsson and Macdonald, 1996). A negative effect of foxes on mink is therefore most likely to take the form of indirect competition for food and mink harassment. An increase in food abundance (natural and man induced), probably positively affected the arctic fox population which has increased substantially in Iceland (Hersteinsson et al., 2009). Increased number of foxes likely impacted vigilance and feeding behaviour of mink and possibly limited mink access to optimal hunting grounds. It is therefore plausible that from around 2004 foxes may have started to disadvantage mink through intra-guild competition. The diet of arctic foxes (Hersteinsson and Macdonald, 1996) mostly comprises birds (seabirds, terrestrial birds and eiders), which are the same prey groups that showed overall decline in mink diet in this study. As a matter of precedent, it is known that mink (Carlsson et al., 2010) and pine marten *Martes martes* (Lindstrom et al., 1995) suffer from prey competition and intra-guild predation, respectively, by red foxes in Scandinavia.

The decrease in freshwater fish consumption in summer among females (Table 2) and the apparent decrease, albeit statistically non-significant, in fish consumption (which mostly comprised freshwater fish) among males throughout the study period (Fig. 4), might be partially explained by increasing fish mobility as freshwater temperature rose throughout the study period, thus making them more difficult to catch and therefore less accessible (Gerell, 1968; Elliott, 1994). Furthermore, increased difficulty in hunting (more swift) freshwater fish may have prompted a shift among females and coastal males in the warm season towards catching marine fish (see details in Appendices), insofar as coastal sea temperature in the study area did not rise as much as freshwater temperature during the study period.

In summary, circumstantial evidence suggests that minks' access to prey might have decreased during the study period due to intra-guild competition with arctic foxes and increased mobility of freshwater fish as a result of rising air temperature.

Impaired hunting ability

Mink's capability to hunt might be reduced as a consequence of diseases or contaminants. The only well-known disease in wild mink in Iceland is the Aleutian disease, which is fairly widespread but does not seem to affect their survival or fertility (Hersteinsson et al., 2012). It may be that contaminants, e.g. mercury (Hg) and polychlorinated biphenyls (PCB's; Yamaguchi et al., 2003) or undiscovered pollutants, play a role in the population decline or diet changes of mink. However, we have to this date no evidence of any decline in mink's capacity to hunt.

These three possible explanations are non-exclusive and any two or all of them might contribute to our results. Rising numbers of arctic foxes in Iceland may have started to affect mink negatively in the last decade through increasing competition while consequences of climate change simultaneously cascaded through the food web to the American mink. Together, these events may explain the observed diet changes and possibly the reduction in the mink population since 2004. This unforeseen vulnerability may turn out to be helpful to management intended to reduce mink numbers, but raises concerns regarding predator conservation in general. Carnivores in many different ecosystems are facing difficulties in tackling global climate change, habitat destruction and/or overexploitation (Macdonald and Sillero-Zubiri, 2004; Macdonald and Loveridge, 2009). In spite of being a generalist and opportunistic, and conspicuously adaptable, even the mink has not withstood these pressures, which emphasises the danger for other carnivores when facing a 'perfect storm' of different threats.

Acknowledgements

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.mambio.2013.08.002.

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