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Habitat- and sex-related differences in a small carnivore's diet in a competitor-free environment

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Abstract The alien invasive American mink *Neovison vison* is fully established in the low species richness and competitor-free environment of Iceland. This study documents the diversity as well as seasonal and sexual variation in the diet of mink in Iceland based on stomach contents. Seasonal changes mainly reflected variation in abundance of migratory birds and wood mice *Apodemus sylvaticus*. In comparison with mink elsewhere in similar habitats, the mink in Iceland consumed more fish and birds and fewer mammals, which is in accordance with local availability. This reinforces evidence of opportunistic foraging. Females generally ate more fish and fewer birds than males and this might be explained by their smaller body size and possible limitation in catching larger birds. Mink in coastal habitats showed greater sexual differences in diet than mink in riparian habitats, probably reflecting less prey diversity in riparian habitats than coastal ones. This study is an input towards explaining the ecological consequences of sexual size dimorphism and supports the hypothesis that generalist species might be successful invaders due to their capability in utilising new and diverse resources. The mink in Iceland can be regarded as a model for a small-bodied semi-aquatic carnivore away from the confounding effects of inter-specific competition.

Keywords *Mustela vison* · Feeding habits · Diet diversity · Niche breadth · Sexual size dimorphism

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Introduction

Members of the family Mustelidae are a successful group of carnivores and most genera are specialised small mammal predators with long and slender bodies, which allow them to enter burrows in search of prey (Brown and Lasiewski 1972; Newman et al. 2011). The American mink *Neovison vison* differs from most of its relatives in being a generalist semi-aquatic species that can forage both in water and on land. Numerous studies of the mink's feeding ecology which have revealed a very broad diet and an opportunistic feeding behaviour have been carried out (Gerell 1967; Birks and Dunstone 1985; Sidorovich 2000; Schuttler et al. 2008; Previtali et al. 1998). These characteristics explain the mink's success as a colonist and now it is considered among the 100 most invasive species (DAISIE 2011) and one of the four most invasive mammals in Europe (Nentwig et al. 2010). Macdonald and Strachan (1999) compiled a database from 22 mink diet studies from the UK, continental Europe and the USA and revealed that fish made up to almost 40% of the mink's diet, mammals comprised a further 25%, followed by crustaceans, birds and a small quantity of insects, amphibians and reptiles. Fish might, however, be underestimated in these analyses as mink studies in their native North America are often performed where mink is thought to be problematic to waterfowl or other harvested species and therefore represents a biased sample (Macdonald and Strachan 1999). Previous diet studies in Iceland based on scats have shown that the most important food source is fish, which comprises 77% of coastal mink's diet and 60% of riparian mink's diet, followed by birds (Skirnisson 1979, 1980).

Niche breadth in mink is broader than in other competing species like otter *Lutra lutra* (Jedrzejewska et al. 2001; Sidorovich et al. 1998; Sidorovich 2000; Bonesi et al. 2004), European mink (Sidorovich 2000) and polecat *Mustela putorius* (Hammershoj et al. 2004; Sidorovich 2000). Sexual differences in diet of mustelids have been found in weasels *Mustela nivalis*, stoats *Mustela erminea* and mink, and males in all species have been reported to consume significantly more lagomorphs than females (see overview in McDonald (2002)) .

The mink has been a component of Icelandic nature since the 1930s. Despite heavy hunting effort, the species has become established and can be found in all habitats that provide food and shelter (Skirnisson et al. 2004). Most feral mink in Iceland are descended from the first mink farm escapees in the 1930s and are of the Mississippi breed (Skirnisson 1993). The mean weight of wild males is 1,183 g in summer and 1,282 g in winter while both summer and winter mean weight of females is 627 g (Skirnisson et al. 2004), which is within the weight range of mink in their native habitats in North America (Dunstone 1993). In comparison, farmed mink body size has increased considerably during the last few decades (Koivula et al. 2010) and is now at least double that of feral mink in Iceland (Hanninen et al. 2008).

Mink habitats in Iceland can broadly be divided into coastal or riparian. Coastal habitats (especially in West Iceland, which can experience up to 6 m of difference between high and low spring tide) usually contain greater prey diversity and the tides bring in fresh supplies twice a day. It might therefore be assumed that prey renewal is lower in riparian habitats. Furthermore, rivers and lakes can freeze over in winter and restrict access to freshwater, while the sea rarely freezes. The Icelandic ecosystem has only one other mammalian predator, the Arctic fox *Vulpes lagopus*, and low species richness compared to many other countries where mink is found. There is little evidence of direct competition between mink and Arctic foxes, although the foxes sometimes chase mink and disturb them while foraging (Hersteinsson 1984). Existing data suggest that the Arctic fox's diet does not significantly overlap that of the mink since the fox is not adept at catching fish (Hersteinsson and Macdonald 1996).

The only non-commensal small mammal in Iceland is the wood mouse *Apodemus sylvaticus*, and even though rabbits *Oryctolagus cuniculus* have recently become feral in Iceland they are only found in small isolated populations. No reptiles, amphibians or large freshwater crustaceans can be found in the wild.

The aim of this paper is to provide information on mink diet in Iceland, which can give valuable insight into the generalistic behaviour of this invasive species. This will facilitate better mink management and evaluation of possible negative impacts on the biota. Outside the UK, little is known about inter-sexual differences in mink diet and this study is an input towards explaining the ecological consequences of sexual size dimorphism. The low species richness in Iceland provides a natural experiment when comparing the diet of the mink across many studies. Thus hypotheses on the causes of variation in food habits of mink can be evaluated in the absence of inter-specific competition. We predicted that (1) there is a difference in diet between habitats due to different prey availability and diversity, (2) there is a difference in diet between seasons due to different prey availability and (3) there is an inter-sexual difference in mink diet in Iceland due to sexual size dimorphism.

Materials and methods

Specimen collection and dietary analysis

We obtained 851 frozen mink corpses (460 males and 391 females) from various coastal and riparian habitats in Iceland (63–67° N, 13–25° W), killed by mink hunters in 1997–2009. Thawed stomachs were weighed and contents were placed in a 2-mm sieve and rinsed thoroughly. The stomach contents were systematically viewed under a binocular microscope and identifiable fragments of bones, feathers, hairs, otoliths, exoskeletons of arthropods and other identifiable remains were examined. Feathers and hairs were identified using Day's (1966) and our own reference collection while fish vertebrae and otoliths were identified using that of Watt et al. (1997) and Härkönen (1986). When feathers were unidentifiable, they were either considered to be from juveniles or from parts of the bird not possessing the diagnostic downy barbules needed for identification. Remains were classified to order and species level if possible.

Division of data

The year was divided into four seasons based on meteorological definitions (Einarsson 1976). The winter months (December–March) have a mean monthly temperature ranging from approx. −1°C to 0°C (The Icelandic Met Office). The days are short, freshwater freezes over and there are no migrant birds present. In spring (April–May), the mean monthly temperature ranges from approx. 2°C to 5°C. Ice starts to melt and migrant birds arrive and begin to nest. Most female mink become pregnant in March–April and give birth in May. The bright summer months (June–August) have the warmest temperatures, with the mean monthly temperature ranging from approx. 8.5°C to 11°C. This is the breeding season of birds and female mink rear their kits. In autumn (September–November), the mean monthly temperature ranges from 1.5°C to 7.5°C, migrant birds leave and juvenile mink disperse.

Home ranges of individual mink in this study are unknown and therefore each individual 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 contain downstream stretches of freshwater rivers) depending on the location of capture.

Graphical and statistical analysis was performed both on fish divided into two groups (marine and freshwater fish) and also as a single group (henceforth termed 'total fish'). Salmonids were considered freshwater fish since mink in Iceland mostly consume parr that have not yet migrated to the ocean (Skirnisson 1980). Similarly, graphical and statistical analysis was performed on birds divided into three groups: seabirds, ducks (Anseriformes) and other birds (mostly terrestrial and semi-terrestrial waders) and also as a single group (henceforth termed 'total birds'). Grasses, aquatic plants, seaweed and unidentified items were noted but not used in calculations.

Statistical methods

The frequency of occurrence ($p=n/N\times100$) for each taxon in all stomachs was determined, where n is the number of stomachs containing a particular prey species and N is the total number of stomachs in the sample (Conroy et al. 2005). Many stomachs contained more than one prey type, resulting in total percentage occurrences greater than 100%. The frequency of occurrence method tends to overestimate the importance of small food items and therefore the proportional weight of each food category was also calculated (Klare et al. 2011). The composition of the diet is thus presented as %mass of each prey group in the total weight of the stomach contents in each habitat (coastal and riparian) for each season. Due to the size difference between the sexes, %mass was calculated separately for the sexes in order to make the results comparable. This was done by calculating the weight of each food category in each animal as a percentage of the mean weight of the intra-sexual stomach contents in each habitat in each season. Food consumption in relation to 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) frequency of occurrence using Fisher's exact test and chi-square test of independence. The statistical programme used was GraphPad Prism version 5.0 for Windows, GraphPad Software, La Jolla, CA, USA.

Calculations of diet diversity and diet overlap

Diet diversity was measured for five food categories in coastal habitats (freshwater fish, marine fish, birds, wood mouse and invertebrates) and four food categories in riparian habitats (freshwater fish, birds, wood mouse and invertebrates) in accordance with Brzezinski (2008), Hammershoj et al. (2004) and Schuttler et al. (2008). Diet diversity was calculated using Levins' standardised niche breadth formula (Krebs 1999):

$$B_A = \frac{\frac{1}{\Sigma p_i^2} - 1}{n - 1}$$

where p_i is the proportion of a given prey group in mink's diet and n is the number of possible resource states. Niche breadth depends on the number of resource states, ranging from 0 to 1, with 1 indicating the broadest niche.

Diet overlap (O_{jk}) between the sexes was calculated using Pianka's adaptations of MacArthurs and Levin's formula (Krebs 1999; Pianka 1973):

$$O_{jk} = \frac{\sum_j^n p_{ij} p_{ik}}{\sqrt{\Sigma_j^n p_{ij}^2 \Sigma_j^n p_{ik}^2}}$$

where j and k refer to the two sexes under comparison and n is the total number of resource states. The index ranges from 0 (no overlap) to 1 (complete overlap).

The software Ecological Methodology, Version 6.1 (Kenney and Krebs 2002), was used to measure niche breadth and diet overlap. We used %mass of each prey type, but in order to facilitate comparison with some other studies we also calculated diet diversity using frequency of occurrence per stomach. Considerable differences have been detected in niche breadth and diet overlap depending on which methods are used for determining diet (Klare et al. 2011) and values obtained with frequency are usually higher than with volume/mass.

Results

Of 851 mink stomachs obtained in 1997–2009 (Fig. 1), 636 contained prey items, of which 327 were from males and 309 from females. Overall, when weighted for sample size and length of season, fish was the most important part of the diet (50.2% mass), followed in descending order by birds

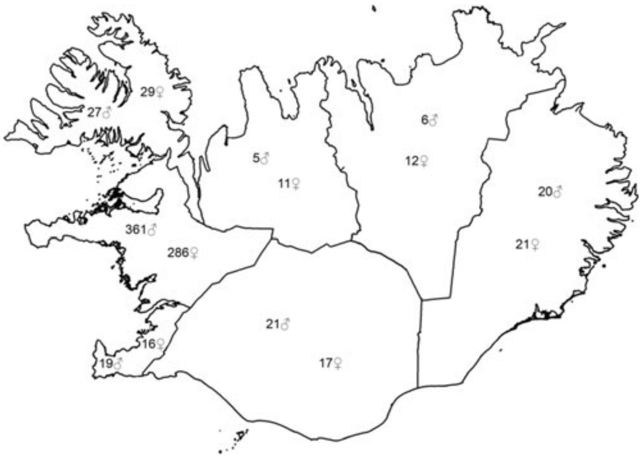

Fig. 1 Number of mink stomach samples in different parts of Iceland

(33.2%), wood mice (9.8%) and invertebrates (6.8%). Analysis by habitat, sex and season showed considerable variation between categories (Fig. 2). Detailed results showing sample sizes, %mass and frequency of occurrence of individual prey species in four seasons for both sexes in two habitats can be found in Appendices 2–5.

Niche breadths in the two habitats were markedly different, with coastal habitats showing fluctuating niche breadth and diet overlap with season while the values were more stable in riparian habitats and similar between the sexes (Fig. 3). Details on diet diversity for both %mass and frequency of occurrence are shown in Appendix 1 to give further comparison with other studies.

No seasonal variation in fish consumption was found in coastal males while fish consumption by coastal females (frequency of occurrence) and riparian mink of both sexes (%mass) varied significantly (Fig. 2; Table 1). Coastal females consumed more total and marine fish than males in all seasons combined. When seasons were tested separately, sex-related variation was found in spring and summer for total fish and winter and spring for marine fish (Fig. 2; Table 2). No significant sexual variation was found in the consumption of freshwater fish in coastal habitats and no sex-related differences were found in riparian mink fish consumption.

No seasonal variation in bird consumption was found in coastal males but coastal females and riparian mink of both sexes showed seasonal variation in consumption of birds (Fig. 2; Table 1). The females consumed fewer birds than

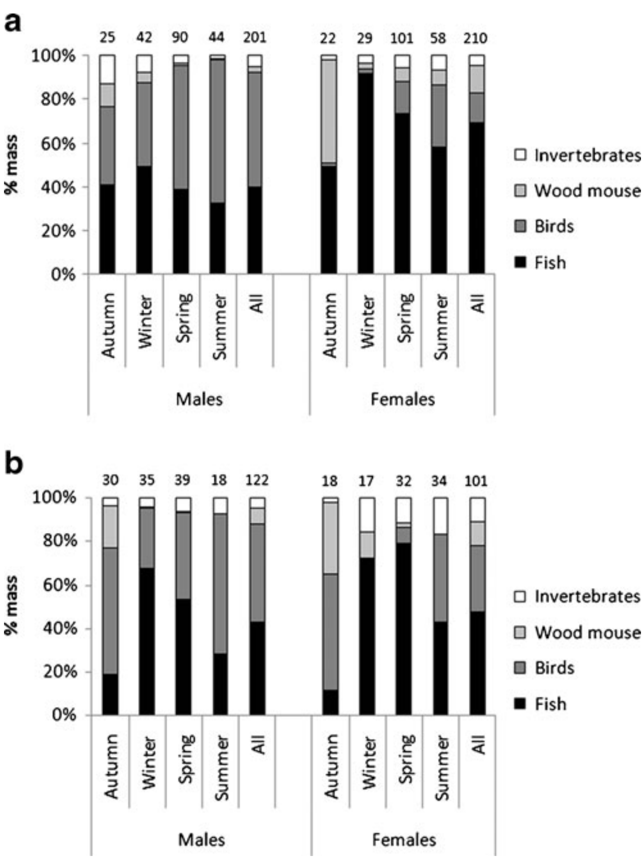

Fig. 2 Main prey groups (%mass) in the diet of male and female mink in all seasons in **a** coastal habitats and **b** riparian habitats in 1997–2009. *Numbers* above the columns indicate sample size

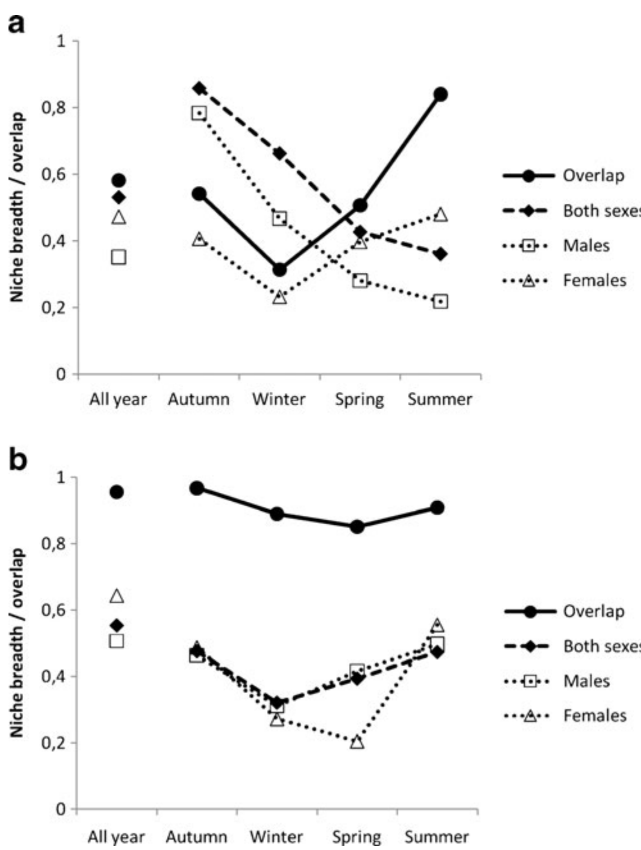

Fig. 3 Niche breadth (*broken lines*) and diet overlap (using %mass) of mink in **a** coastal habitats and **b** riparian habitats over the whole year and by season

Table 1 Test statistics for seasonal differences in prey consumption (Kruskal–Wallis one-way analysis of variance test for %mass) in males and females in coastal and riparian habitats

	Coastal males		Coastal females		Riparian males		Riparian females	
Total fish			/**		P=0.0005/***	↑ W/Sp and ↓ A	P=0.004/**	↑ W/Sp and ↓ A
Freshwater fish					P=0.0046/***	↑ W/Sp and ↓ A	P=0.0154	↑ Sp and ↓ A
Total birds			P=0.0002/**	↑ S and ↓ A/W/Sp	P=0.0022/**	↑ S and ↓ W/Sp	P=0.0016/**	↑ S and ↓ W/Sp
Seabirds			P=0.0422/*	No difference				
Other birds			P=0.0104/*	↑ S and ↓ Sp	P=0.0003/***	↑ A and ↓ W/Sp		
Mouse	P=0.0026/***	↑ A	P=0.0001/***	↑ A	P=0.0001/***	↑ A	P=0.0048/*	↑ A
Invertebrates					/*			

Level of significance was $P<0.05$. Test statistics for frequency of occurrence are indicated

Arrows indicate high or low consumption of prey item (Dunn's post hoc tests $P<0.05$) in the seasons, *A* autumn, *W* winter, *S* summer, *Sp* Spring

*$P\leq0.05$; **$P\leq0.01$; ***$P\leq0.001$

males in winter and spring (Fig. 2; Table 2). Overall in coastal habitats, males consumed more birds than females, and sex-related differences were found in autumn, winter and spring for total birds, in winter for seabirds and in spring for ducks. The only sex-related difference found in riparian areas was in duck consumption, where males consumed more than females did in spring (Table 2).

Seasonal variation was found in mouse consumption of males and females in both habitats (Fig. 2; Table 1), and even though females tended to consume more wood mice than males in autumn (Fig. 2), no sex-related differences were found in any season.

The frequency of occurrence of invertebrate consumption by riparian males varied seasonally. Females in coastal habitats consumed more invertebrates than males in summer and in riparian habitats females ate more invertebrates than males in all seasons (Fig. 2; Table 2).

Discussion

It has been hypothesised that generalist species might be successful invaders due to their capability in utilising new and diverse resources (Sol 2007). Because of the general success of American mink as an invader, mink diet studies are relevant to put this hypothesis to the test. The findings of this study strongly underline the generalistic behaviour concerning mink food choice and therefore support the hypothesis, as do previous studies on mink diet (e.g. Jedrzejewska et al. 2001; Sidorovich 2000; Bonesi and Macdonald 2004).

This study revealed great variation in individual stomach contents within habitats, seasons and sexes. Therefore, a large sample size, as presented here, is essential to describe accurately the diet of this species and make meaningful comparisons.

The results of this study revealed diet diversity in different habitats and inter-sexual differences in mink diet in Iceland. Furthermore, it showed that seasonal changes in mink diet coincided with variation in abundance of migrating birds, seasonal access to fish due to water temperature and seasonal availability of wood mouse.

Diet diversity in different habitats and seasons

There were great differences in mink diet between habitats and seasons which are in accordance with our first and second predictions. Seasonal fluctuations in the mink's diet in Iceland were similar between the sexes in riparian habitats but much more intense between the sexes in coastal habitats, where male's diet was quite stable throughout the year. In riparian habitats, furthermore, the sexes seemed to be utilising the same resources while males and females in coastal habitats were often consuming different prey. Riparian females in autumn, contrary to their coastal counterparts, consumed large quantities of birds (mostly waders) like the males and it is possible that these birds were not killed in autumn but rather cached in summer for later consumption. Another explanation might be that waders congregate in flocks before migrating to their winter grounds, of which the mink can take advantage. Despite the lack of statistical support, there are indications (Fig. 2b) that males and females in riparian habitats were consuming more birds in autumn than in winter and spring. The lack of statistical difference is due to the fact that some mink had consumed large quantities of birds in autumn while others had no bird remains in their stomachs, indicating that some riparian mink specialised in bird consumption in autumn, feeding mostly on waders. It has been suggested that coastal habitats are of superior quality and more productive of food than any freshwater body

Table 2 Test statistics for sex-related differences in prey consumption (Mann–Whitney *U*-test for %mass and Fisher's exact test and chi-square test of independence for frequency of occurrence) in different seasons in coastal and riparian habitats

	Autumn		Winter		Spring		Summer		All seasons	
	%mass	Frequency	%mass	Frequency	%mass	Frequency	%mass	Frequency	%mass	Frequency
Coastal										
Total fish					P=0.0033	P=0.0043	P=0.0328		P<0.0001	P=0.0003
Marine fish			P=0.0199	P=0.0367	P=0.0062	χ^2=4.069, P=0.0437[a]			P=0.0001	P=0.0009
Total birds	P=0.0467		P=0.0239	P=0.038	P<0.0001	P=0.0001			P<0.0001	P<0.0001
Seabirds			P=0.0224	P=0.0365					P=0.0225	P=0.0132
Ducks					P=0.0166	P=0.008			P=0.002	P=0.001
Invertebrates							P=0.0077	P=0.0077		
Riparian										
Ducks					P=0.0383	χ^2=4.679, P=0.0305[a]				
Invertebrates									P=0.0445	

Level of significance was P<0.05

[a] Chi-square was calculated when Fisher exact test was not significant

(Dunstone and Birks 1985; Clode et al. 1995). The annual niche breadths for both sexes combined were very similar in both habitats. The seasonal range for males in coastal habitats was larger than for females in coastal habitats and both sexes in riparian habitats. Coastal mink consumed more species than riparian mink but exploited them less evenly. Because of this, niche breadths calculated for both sexes collectively over the whole year would fail to reveal the differences between sexes, seasons and habitats, which underlines the importance of segregating the data. Females seem to have similar niche breadths in the two habitats and the seasonal quantities of main prey groups were similar except in autumn when their diets were different despite similar niche breadth values.

The results of this study indicate a difference between the habitats; prey abundance is not known but the difference can be explained with different food availability between the two habitats. Coastal males and females seem to be able to choose alternative prey, suitable for each sex, as low diet overlap suggests, but riparian mink of both sexes utilise the same resources, increasing diet overlap and inter-sexual competition. Furthermore, seasonal fluctuations in niche breadths of the sexes vary together in riparian habitats, while in coastal habitats there are large fluctuations between seasons in the niche breadth of males, independent of that of females, suggesting a different reaction to variation in food availability.

In previous studies based on scats, Skirnisson (1980, 1979) found that on a yearly basis about two thirds of the Icelandic mink's diet consisted of fish, with more fish consumed by coastal mink than by mink in riparian habitat. In contrast, we found that fish composed a little less than half of the diet of both sexes in riparian habitat and of males in coastal habitat; in coastal females, however, fish composed two thirds of the diet. The unlike results between the two Icelandic studies might be explained by the different methodologies employed. Most of the scats in Skirnisson's (1979, 1980) studies were collected in two small study areas (1.5-km coast and 4.5-km riverbank) and may not have been representative for the country as a whole. The diet choice of coastal females in our study is however similar to the overall results of Skirnisson, which might indicate that Skirnisson's sampling could have been biased towards female scats. Another possible explanation for the different results is that prey species dynamics and abundance may have changed in the last 30 years. A year-dependent analysis on mink diet in the Snæfellsnes Peninsula is indeed currently being conducted by the authors of this study and will be published separately.

Sex-related differences

This study revealed sex-related differences in diet in accordance to our second prediction, mostly in coastal habitats where females consumed more fish and fewer birds than males. The vast difference in bird consumption between the coastal sexes in autumn and winter may indicate that birds are not accessible for females in those seasons or not their prey of choice, whereas fish and possibly mice appear to be preferred or more accessible.

Fish have less mobility in the cold months and are thus easier to catch than in warmer months (Gerell 1968), but increased fish predation in winter may also result from the lack of alternative prey (Dunstone and Birks 1987). This can be seen in coastal females and riparian mink of both sexes in this study, whose fish consumption is high in winter. In comparison with mink elsewhere in similar habitats but in competition with other mustelids (Dunstone and Birks 1987; Akande 1972; Salo et al. 2010; Macdonald and Strachan 1999), the mink in Iceland eats in general more fish and birds and fewer mammals, which is in accordance with the availability of local prey species. Marine fish can most easily be caught in rocky shores where the tides bring in fresh supplies to rock pools twice a day. For pregnant or lactating females, access to such areas may prove vital since it may not be energy-efficient for them to forage for birds over large areas but the opposite may be true for larger-bodied males.

It may be assumed that most of the ducks preyed upon in coastal habitats were the large (2 kg) eider *Somateria mollissima* since they are by far the most abundant duck in Iceland (Jonsson et al. 2009). Males seem to be more efficient than females at hunting ducks and seabirds in winter and spring, but it is also possible that some of these birds were not hunted but rather scavenged on the coast. The wood mouse population peaks in both sexes' diet and both habitats in autumn, which is in agreement with studies on wood mouse population dynamics (Unnsteinsdottir and Hersteinsson 2009). The wood mouse is found in much lower densities in Iceland than in northern Europe (Montgomery 1989; Gorman and Ahmad 1993) where other small mammal species are also present (Salo et al. 2010; Birks and Dunstone 1985). It is probably more energy-efficient for mink to switch to other more abundant prey when mouse population density is low.

A high proportion of the mink population in autumn are dispersing juveniles, which are naive and still not fully grown and have not yet established their own home ranges. It seems to be suitable for small juvenile females to prey upon the plentiful wood mice in autumn, which explains the different niche breadth values of the coastal sexes in autumn. In winter, the sexes were consuming very different food by the coast, males mainly eating birds and females marine fish, which is the reason for the very low diet overlap between the sexes in that season. This may be regarded as an adaptive side effect of body size dimorphism (Birks and Dunstone 1985; Moors 1980; Thom et al. 2004).

Sex-related differences in diet have been noted in weasels, stoats and mink (see comparison of studies in McDonald 2002) and such variation was usually caused by differential predation on lagomorphs and/or rodents. Very few studies have been conducted on sexual variation in mink diet but Sealander (1943) found sex-related variation in winter consumption of muskrats *Ondatra zibethica zibethica* and Birks and Dunstone (1985) found significant differences in lagomorph consumption between sexes in most seasons; in both studies, males consumed more medium-sized mammals than females. Our study shows similar seasonal patterns in diet overlap between the sexes in coastal habitats as found by Birks and Dunstone (1985) where diet overlap was very high in summer but lower in other seasons. Hammershoj et al. (2004) did not find sex-related differences in mink diet but they speculated whether the results would have been different if lagomorphs had been available in their study areas. Feral rabbits are only found locally in close proximity to human habitation in Iceland and were not consumed by mink in this study; nevertheless, a considerable sexual variation in diet was found in coastal areas. We suggest that the sex-related differences observed in the diet of coastal mink in Iceland in the absence of lagomorphs is driven by sexual dimorphism in body size in areas with high spatial variability of prey types available, while lack of alternative prey forces the sexes to utilise a similar composition of prey species in riparian habitats. Due to the lack of inter-specific competition in Iceland, mink are free to roam terrestrial habitats in search of food, especially during the influx of migrating birds in spring and summer. Because of the limitations set by the position of female den and litter, this applies especially to males and might explain some of the sex-related difference in diet in Iceland and the difference between allopatric mink in Iceland and Denmark. Mink in the Thy area, Denmark (Hammershoj et al. 2004), were sympatric with other mustelid species, no lagomorphs were present and no difference was found in diet between the sexes, a situation similar to that found in the allopatric riparian mink in Iceland.

This study gives further evidence of the generalist feeding behaviour of the species; the mink in Iceland, especially in coastal areas, shows sex-related differences in diet in the absence of inter-specific competition and medium-sized mammal prey, showing that neither is a necessary prerequisite for sexual variation in diet.

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