

Effects of home-range characteristics on the diet composition of female American mink in the Baltic Sea archipelago

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Predator home-range size may serve as a proxy of resource abundance and spatial structure of home range may also reveal information about diet composition of predators. We studied the diet of American mink *Mustela vison*, an introduced predator in Europe, to explore diet composition and to examine the association of diet with home-range characteristics. We collected scats of radio-tracked mink (two males and nine females) in summers 2004–2005 in the Archipelago Sea, SW Finland. The most important prey groups were fish (33% occurrence), birds (28%) and small mammals (mainly voles; 15%). The proportion of small mammals in female mink diet correlated positively with home-range size, which indicates that larger home ranges include larger islands, where vole populations are more persistent. Our results highlight the importance of fish as main prey for survival and invasion of mink in the outer archipelago, subsidising mink impact on other prey.

Introduction

According to conventional foraging theory, the prey preference of a predator is reliant only upon the predator's active choice of prey (Stephens & Krebs 1986). However, predator behaviour will also be affected by prey availability; for example low resource abundance may force an individual to roam on a larger home range. The home-range size of wolves *Canis lupus* correlates negatively with prey abundance (Jędrzejewski *et al.* 2007),

and lynx *Lynx lynx* home ranges increase with decreasing ungulate abundance (Schmidt 2008). Therefore home-range size could be used as a proxy of home-range resource availability.

In a more detailed level, home-range characteristics such as proportions of different habitat in home range, may deliver information of more specific predator diet composition. Such studies are few, they but have, for example, recorded a change in hunting habitat and diet breadth of Eurasian kestrels *Falco tinnunculus*: in response

to a decline of its main prey species, *Microtus* voles, kestrels hunted more in forests and preyed more upon birds and insects (Korpimäki 1985, 1986). The proportion of wood rats *Neotoma* sp. in the diet of northern spotted owls *Strix occidentalis caurina* correlated positively with the use of habitat edges and a smaller home range, whereas owls preying mostly on northern flying squirrels *Glaucomys sabrinus* had a large home range and did not prefer edges (Zabel *et al.* 1995). On the more applied side are studies linking habitat characteristics with the probability of large carnivores attacking domestic animals (Stahl *et al.* 2001, Treves *et al.* 2004). For example, Treves *et al.* (2004) found that wolf predation risk on cattle was higher in townships with more pastures and less coniferous forests and crop lands.

Introduced predators usually have a more suppressive impact on native prey populations than native predators (Salo *et al.* 2007 and references therein), probably because of the varying levels of prey naïveté (Banks & Dickman 2007). Thereby the effect of alien predation has often been most dramatic in insular ecosystems, even resulting in extinctions of some species (Courchamp *et al.* 2003, Blackburn *et al.* 2004). One example of a successful invasive species is the American mink *Mustela vison* (hereafter mink), a semi-aquatic generalist predator with very versatile habitat requirements and high reproductive potential (Dunstone 1993). Originally a North American mustelid, it was introduced to Europe as a fur animal in the 1920s (Dunstone 1993). Feral mink have since become established throughout Europe, and mink populations are also known from South America and Asia (Bonesi & Palazon 2007). Across its distribution, mink diet reflects opportunistic predation on available prey species, and therefore consists of fish, birds (including their eggs and chicks), amphibians, crustaceans, insects and mammals (ranging from small mammals to muskrats *Ondatra zibethicus* and hares *Lepus* sp.) in different proportions, depending on the local and seasonal abundance of prey (Dunstone 1993 and references therein). In its introduced range, mink predation has been shown to affect various mammal, bird and amphibian species (reviewed in Macdonald & Harrington 2003, Bonesi & Palazon 2007, Banks *et al.* 2008).

Feral mink were first observed in Finland in the 1930s (Westman 1966), and in the 1970s mink invaded the whole country (Kauhala 1996). Mink are common even in the southwestern archipelago of Finland (Kauhala 1996), the outer zone of which comprises of small islands and islets with scarce vegetation. There mink home ranges consist of groups of small islands, as most single islands are not large enough to support a mink year round. Fish is the staple food for mink year round, whereas birds in the diet peak in June and the proportion of mammals varies between years as vole populations increase and decline (Niemimaa & Pokki 1990). Mink have been shown to negatively affect the populations of voles (Banks *et al.* 2004, Fey 2008), common frogs *Rana temporaria* (Ahola *et al.* 2006) and most of the breeding bird species (Nordström *et al.* 2002, 2003, Nordström & Korpimäki 2004) in the outer archipelago. Colonial seabirds like the black guillemot *Cepphus grylle* have been particularly negatively affected (Hario 2002, Nordström *et al.* 2002).

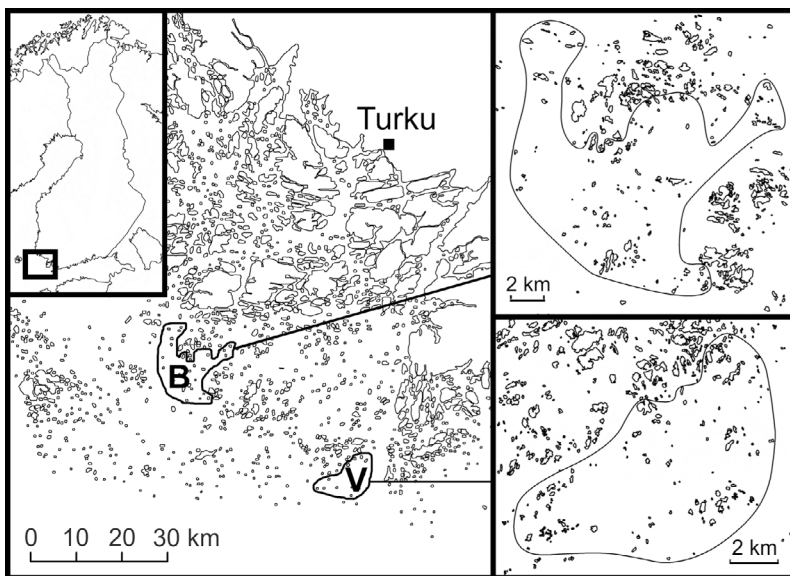
While the diet of mink in the outer archipelago of the Baltic Sea is quite well known, there is no knowledge how island and therefore home-range characteristics determine the prey choice of mink. For example, bird colonies tend to situate on small, isolated islands, whereas non-colonial birds nest scattered around the islands (Nordström & Korpimäki 2004). Small mammals occur patchily (Banks *et al.* 2004), whereas fish are widely available. We set out to study (1) the summer diet composition of mink and (2) the relationship between mink diet and home-range characteristics in the outer archipelago. We predict that mink diet composition will reflect the size, structure and isolation of the home range. For example, as larger islands tend to support more stable vole populations (Pokki 1981), therefore mink on such islands should consume more voles.

Material and methods

Study areas and prey species composition

The study was conducted in two areas, Brunskär in Korppoo (60°01'N, 21°23'E) and Vänö in

Fig. 1. Location of the two study areas in the Archipelago Sea, SW Finland, where American mink were radio-tracked in 2004–2005. B = Brunskär and V = Vänö. (©National Land Survey of Finland 763/MYY/06).



Dragsfjärd (59°48'N, 22°11'E), which are situated 50–60 km off mainland on both state and private lands in the Archipelago National Park joint working area in the Baltic Sea, SW Finland (Fig. 1). Brunskär covers 117 km², with 3.4 km² land area and a mean island size of 1.9 ha (range 0.16–24 ha). Vänö covers 60 km², with 2 km² land area and a mean island size of 1.1 ha (range 0.15–21 ha). Most islands are small and rocky, and their sparse vegetation is characterised by grasses (Poaceae, Cyperaceae) and a shrub layer consisting of bog bilberry *Vaccinium uliginosum*, heather *Calluna vulgaris*, crowberry *Empetrum nigrum*, and juniper *Juniperus communis*. A few of the largest islands have solitary trees, mainly pine *Pinus sylvestris*, rowan *Sorbus aucuparia*, and alder *Alnus glutinosa*.

Potential prey items for mink in these areas include mammals, birds, fish and amphibians (Niemimaa & Pokki 1990). Voles are the only mammals common in the outer archipelago, with field vole *Microtus agrestis* being the dominant species (Pokki 1981). Bank voles *Myodes glareolus* and shrews *Sorex* spp. are scarce, and mountain hares *Lepus timidus* may seldom occur on larger (≥ 4 ha) forested islands. The amphibians include common frog *Rana temporaria*, common toad *Bufo bufo* and common newt *Triturus vulgaris*.

The availability of birds is highly seasonal, as

it is connected to the nesting period which lasts from the beginning of May to the end of July. The most common breeding bird species are common eider *Somateria mollissima*, common gull *Larus canus*, herring gull *Larus argentatus* (in a few large colonies), and arctic tern *Sterna paradisaea*. A few species of passerines are also common: wagtail *Motacilla alba*, rock pipit *Anthus petrosus* and meadow pipit *Anthus pratensis* nest under rocks and in the shrub layer of the islands. Birds in both study areas are surveyed yearly by Metsähallitus Forest and Park Service.

The most common fish species in our study areas are perch *Perca fluviatilis*, Baltic herring *Clupea harengus membras*, roach *Rutilus rutilus*, flounder *Platichthys flesus* and whitefish *Coregonus lavaretus* (Ädjers *et al.* 2006). Other possible prey species for mink include e.g. viviparous blenny *Zoarces viviparus* and ide *Leuciscus idus*. Although numerous, Baltic herring is a pelagic species and therefore mostly unavailable for mink, which tends to search and detect fish from the shore before actually entering the water (Dunstone 1993).

There are essentially no other mammalian predators in our study areas besides mink, as red foxes *Vulpes vulpes* and raccoon dogs *Nyctereutes procyonoides* are extremely rare in the outer archipelago. The only other common pred-

ator in the study areas besides mink is the white-tailed sea eagle *Haliaeetus albicilla*. Other raptors visit the islands during spring and autumn migration.

Mink radio tracking and scat analysis

We trapped and radio-tracked mink in June–August 2004 in Vänö and in May–July 2005 both in Vänö and in Brunskär (Table 1). Mink were caught either in baited box traps or by flushing with a leaf-blower (*see* Nordström *et al.* 2002, 2003 for details), and they were anaesthetised immediately after capture with a combination of medetomidine hydrochloride (Domitor® 1 mg ml⁻¹, Orion Pharma, Espoo, Finland) and ketamine (Ketalar® 50 mg ml⁻¹, Pfizer, Helsinki, Finland). The animals were sexed, weighed, and fitted with a waterproof radio transmitter attached to a collar (Teflon Collar, model TW-4, Biotrack Ltd., Poole, UK). The maximum lifetime of the transmitters was three months. The weight of the collar was ca. 10 g which was 2% of the weight of the lightest female in the study. After handling, the anesthesia was reversed with atipamezole hydrochloride (Antisedan® 5 mg ml⁻¹, Orion Pharma), and we allowed the animals to recover for about 20–30 minutes before release at the place of capture. All animals

recovered well from the treatment. Permission to catch and anaesthetise animals was held by the Lab-animal care and use committee at the University of Turku.

We located radio-collared mink at least twice per day (usually in the morning and in the evening) using receivers (Sika, 138–174 MHz, Biotrack Ltd.) connected to three-element Yagi antennas (Biotrack Ltd.). Mink scats were collected from den sites found during trapping and radio tracking. We collected only fresh scats that could be linked to known mink individuals (e.g. male home ranges can overlap several female home ranges); weathered scats were not collected. From a total of 20 radio-tracked mink, 11 individuals (nine females and two males) yielded enough data from both radio tracking and diet composition to be included in the analysis (Table 1). In addition to these radio-tracked individuals, scats from one female with kits in the area of Brunskär were included in the overall diet analysis (Table 2).

For prey identification the scats were soaked in a detergent solution overnight and then sieved (mesh sizes 5 mm and 0.5 mm). The remaining material was dried at 50 °C for 24 hours and then weighed. We identified mammalian preys to the species level using hairs (Teerink 1991) and teeth, while birds were identified from feather remains either as waterfowl (Anseriformes), pas-

Table 1. Summary table of American mink studied in the Archipelago Sea, SW Finland in summers 2004–2005. The table shows study year and area, mink id (sex: M = male, F = female, and an identification number), duration of radio tracking, mink home-range size (land area of all islands included in the home range), mean distance between islands in home range, number of islands in home range, the number of islands and the land area of islands within 1 km radius from home-range boundaries.

Year	Area	Mink ID	Tracking time (days)	Home-range size (land area, ha)	Distance between islands (m)	No. of islands	No. of islands 1 km radius	Land 1 km radius (ha)
2004	Vänö	M3	64	51.3	1725.7	30	22	10.6
		F2	22	14.1	263.5	6	25	23.3
		F6	27	5.1	235.4	7	28	20.0
2005	Vänö	M15	53	10.9	1133.6	9	9	27.2
		F16	53	6.6	692.0	2	27	43.4
		F17	6	11.8	15.2	2	27	28.8
		F18	52	4.1	0	1	26	12.0
2005	Brunskär	F20	53	3.9	103.0	2	7	15.6
		F21	39	8.9	429.7	3	4	5.5
		F25	33	15.3	446.3	10	26	12.1
		F26	35	4.9	0	1	11	97.5

serines (Passeriformes), or waders, larids and allies (Charadriiformes) using downy barbules (Day 1966). We used scales and bones to identify fish to either order or species level with the key of Steinmetz and Müller (1991) and a reference collection. We also distinguished insects, crustaceans and other material. After identification the prey items were counted and weighted.

We present the data on mink diet in four ways: (i) ‘% occurrence’ is the percentage of a prey item of all observed prey items; (ii) ‘% scats’ is the percentage of scats containing a particular prey item of all scats; (iii) ‘% dry weight’ is the percentage dry weight of a prey item of the total dry weight of all scats; and (iv) ‘% biomass’ is the percentage fresh weight of a prey item of the total fresh weight of consumed prey. We converted dry weights to ingested biomass using correction factors (CFs) obtained

from Fairley *et al.* (1987) (rodents 9, birds 12, fish 25, crustaceans 7, gastropods 7), Brzeziński and Marzec (2003) (rodents 17.3, small birds 17.2, chicken 41.3, fish 30.8) and Lockie (1961) (insects 5). For passerines we used the CF for small birds, for waterfowl the CF for chicken, and for waders, larids and unidentified birds we used the mean of CFs for small birds and chicken from Brzeziński and Marzec (2003).

Mink home ranges

Home-range boundaries for each mink were calculated as minimum convex polygons (MCP) with Ranges 6 (Anatrack Ltd., Poole, UK) and plotted on a raster map in MapInfo (MapInfo Professional 7.5, MapInfo Corporation, Troy, New York, USA). We used all radio locations

Table 2. The overall diet of American mink ($n = 12$) in the Archipelago Sea in summers 2004–2005. The data is presented as (i) % occurrence = percentage of a prey item of all observed prey items (number of occurrences $n = 378$); (ii) % scats = percentage of scats containing a particular prey item of all scats (number of scats $n = 184$); (iii) % dry weight = percentage weight of a prey item of the total dry weight of all scats (total dry weight 100.6 g); (iv) % ingested biomass = percentage fresh weight of a prey item of the total fresh weight of consumed prey. Fresh weight was obtained by multiplying the dry weight of each prey item by a correction coefficient.

Prey items	% occurrence ($n = 378$)	% scats ($n = 184$)	% dry weight	% ingested biomass ¹	% ingested biomass ²
Field vole <i>Microtus agrestis</i>	9.5	19.6	18.1	14.9	12.1
Bank vole <i>Myodes glareolus</i>	0.8	1.6	1.5	1.2	1.0
Shrews <i>Sorex</i> spp.	0.8	1.6	1.5	1.2	1.0
Unidentified mammals	4.1	8.2	7.5	6.2	5.0
Mammals total	15.2	31.0	28.6	23.6	19.2
Perch <i>Perca fluviatilis</i>	17.2	35.3	18.7	20.6	22.3
Ruffe <i>Gymnocephalus cernuus</i>	3.2	6.5	3.5	3.9	4.2
Viviparous blenny <i>Zoarces viviparus</i>	0.9	1.6	0.9	1.0	1.1
Sculpins (Cottidae)	1.1	2.2	1.2	1.3	1.4
Flatfish (Pleuronectiformes)	0.5	1.1	0.6	0.7	0.7
Sticklebacks (Gasterosteidae)	0.4	0.5	0.3	0.3	0.4
Carps and minnows (Cyprinidae)	0.3	0.5	0.3	0.3	0.4
Unidentified fish	9.2	19.0	10.0	11.0	11.9
Fish total	32.8	66.8	35.5	39.1	42.4
Waterfowl (Anseriformes)	4.2	8.7	4.9	5.4	7.8
Passerines (Passeriformes)	2.6	6.5	3.1	3.4	2.1
Waders and larids (Charadriiformes)	3.1	5.4	3.7	4.1	4.2
Unidentified birds	18.5	37.5	21.1	23.2	23.9
Birds total	28.4	58.2	32.8	36.1	38.0
Crustaceans	8.3	17.9	0.8	0.5	0.2
Insects	5.8	10.9	1.1	0.7	0.2
Unidentified/miscellaneous	9.5	19.6	1.2	–	–

¹Fairley 1987, ²Brzeziński & Marzec 2003.

for defining home-range boundaries. Incremental area analysis showed that MCPs tended to stabilise after on average 15 locations (range 6–34), while the mean number of locations taken per animal was 20 (range 8–36).

Because of the patchy nature of archipelago mink home ranges, all islands with radio locations and within or crossing the minimum convex polygon were included in the home range. We then calculated mink home-range size as the sum of land area (ha) of all islands in the home range. We assumed that a mink located on an island utilized the whole island, and this was often confirmed by radio tracking. One exception was mink F16 (Table 1), which used a small part of a large island of 20.6 ha, and therefore only this 2.3 ha part was included in home-range size calculations. We also calculated other home-range characteristics, such as the number of islands and the mean distance (m) between islands included in the home range. We described the isolation of mink home ranges from the surrounding archipelago using the number and land area of islands within 1 km radius of home-range boundaries (Table 1). Most daily movement distances (straight-line distance between evening and morning locations) of radio-tracked mink were less than 1 km, therefore we chose that distance to describe isolation.

Statistical analyses

We conducted a compositional analysis (Aitchison 1986, Aebischer *et al.* 1993) using multivariate regression to test the effects of different home-range characteristics on mink diet composition, which was described as ‘% occurrence’ of the three main prey groups (fish, birds, mammals). To overcome the linear dependence of these groups (the typical unit-sum constraint problem of compositional data; Aitchison 1986), we calculated log-ratios by first dividing the % occurrences of each group by the occurrence of “other” group and then taking the natural logarithm (ln) of the resulting ratios (Aebischer *et al.* 1993). For calculations, we replaced zero % occurrences of mammals in the diet of three females by 0.001 which is considerably smaller than the smallest recorded % occurrence of

0.053. We then used the log-ratios as response variables in a multivariate regression with all the home-range characteristics as explanatory variables. For each explanatory variable the procedure yields Wilks’ λ value, which measures the proportion of unexplained variance in the combination of dependent variables. The two study years and two study areas were pooled for the analysis, as each mink was followed for only one summer and in one area. The level of significance was set at ≤ 0.05 . The explanatory factors did not correlate significantly with each other (Spearman rank correlation: r_s range –0.13 to 0.61, $P > 0.08$, $n = 9$).

We built our model with females only, as including males introduced large variation into the data. Male mink occupy larger home ranges than females (Gerell 1970, Birks & Linn 1982, Yamaguchi & Macdonald 2003, Salo *et al.* 2008), and they are free to move around their ranges, whereas female movements are restricted because of kits. The diet of mink males may also differ from that of females due to sexual size dimorphism (Birks & Dunstone 1985), and because our dataset included only two males, the exclusion of them was justified. We tested for differences between areas and sexes in the proportions of mammals, birds, fish and other prey in the diet with a likelihood ratio chi-square test. All tests were conducted with SAS Statistical Package, ver. 9.1 (SAS Institute, Cary, NC, USA).

Results

Mink diet

Altogether, analysis of 184 mink scats yielded 378 prey items, i.e. one scat contained on average two prey items. The most important prey group was fish, as 67% scats (123 scats) contained fish remains (Table 2). Birds were the second most important prey group (58% scats), followed by mammals (31% scats). Crustaceans (mainly Bivalvia and *Gammarus* species) and insects (bees, ants or beetles) were found in small amounts in 28% of the scats; however, a few scats consisted exclusively of *Palaemon* spp. Miscellaneous prey items and unidentified

material was found in 20% of scats. Non-food items such as grass were scarce and excluded from the analysis.

Out of all fish prey occurrences ($n = 124$), perch was by far the most important species (53%; Table 2). The only other common species was ruffe (10%), whereas viviparous blenny, sculpins (Cottidae), flatfish (Pleuronectiformes), sticklebacks (Gasterosteidae) and carps (Cyprinidae) represented only 1%–3% each. As many as 28% of fish items remained unidentified. These were probably species which do not possess scales, such as flatfish. On the other hand, the importance of perch might be slightly exaggerated since its scales are very easy to identify.

Out of all bird prey occurrences ($n = 107$), the proportions of ducks (15%), waders and larids (11%) and passerines (9%) were quite equal (Table 2). As many as 65% of bird occurrences were unidentified. These items may include eider, wader and larid chicks, which lack the identifiable downy barbules (Day 1966). Field voles represented 64% of the total 57 mammal occurrences, the rest containing common shrews (5%) and bank voles (5%). Over a quarter (26%) of mammalian items were unidentified, mainly because of lack of identifiable guard hairs.

Mammals occurred more often in mink scats in Vänö than in Brunskär ($G^2 = 7.82$, $P = 0.005$, $n = 184$), while there were no differences in bird ($G^2 = 0.61$, $P = 0.44$), fish ($G^2 = 0.97$, $P = 0.32$) and other prey ($G^2 = 0.48$, $P = 0.49$) occurrences between areas. The scats of the two male mink contained more often mammals ($G^2 = 5.92$, $P = 0.015$, $n = 184$) and birds ($G^2 = 6.79$, $P = 0.009$) and less often fish ($G^2 = 4.45$, $P = 0.035$) and other prey items ($G^2 = 6.43$, $P = 0.011$) than those of the 10 females.

In addition to scat analysis, we also found stored prey items and prey remains during mink

radio tracking, identified as mink prey because they mostly were hidden under rocks or juniper bushes. Altogether we found 55 items, of which 46% were fish (25 items including eight flatfish and eight perch), 38% birds (including eight eiders, eider eggs, four small passerines and seven larids), 11% mammals (six voles) and 6% amphibians (two toads and one common frog).

Home-range characteristics and female mink diet

Number of islands in home range and land area within 1 km radius were omitted as nonsignificant factors from the model ($P > 0.29$), while the rest of the factors showed significant associations with diet composition. Home-range size showed an overall significant relationship with mink diet composition (Wilks' $\lambda = 0.10$, $F_{3,3} = 9.28$, $P = 0.050$); more specifically, home-range size was positively related to the occurrence of mammals in the diet, but negatively related to the proportions of fish and birds (Table 3 and Fig. 2a). There was also a significant relationship between mink diet composition and the mean distance between islands in home range (Wilks' $\lambda = 0.09$, $F_{3,3} = 9.61$, $P = 0.048$), which showed a positive association with proportions of all prey groups (Table 3 and Fig. 2b). The number of islands within 1 km radius was also related to mink diet composition (Wilks' $\lambda = 0.07$, $F_{3,3} = 13.43$, $P = 0.030$), showing a slight negative association with mammals and birds and a positive association with fish (Table 3 and Fig. 2c). Because of the strong albeit nonsignificant correlation between home-range size and the distance between islands within home-range boundaries ($r_s = 0.58$), we also omitted the latter factor from the model. Thereafter the results showed signifi-

Table 3. Parameter values from a multivariate regression on log-ratio transformed occurrences of the three main prey groups (mammals, fish and birds) in the diet of nine female American mink in the Archipelago Sea in summers 2004–2005. P values denote possible differences in parameter values between prey groups.

Variable	Mammals	Fish	Birds	Wilks' λ	F	num df, den df	P
Home-range size	0.5105	-0.0072	-0.0246	0.27	5.44	2, 4	0.072
Distance between islands	0.0024	0.0009	0.0014	0.85	0.34	2, 4	0.730
No. islands within 1 km range	-0.0607	0.0047	-0.0282	0.29	4.88	2, 4	0.085

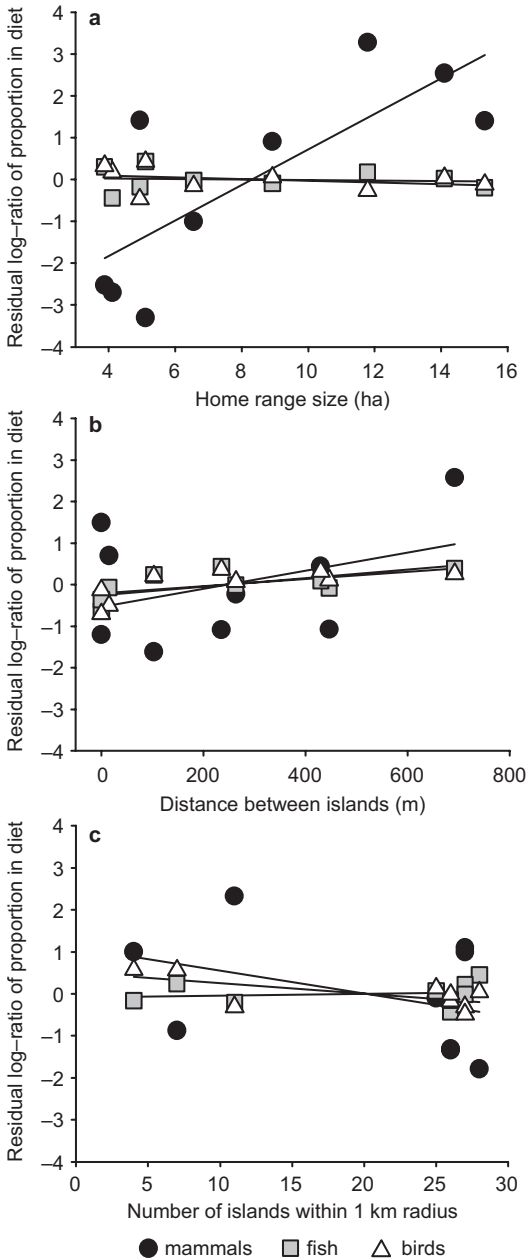


Fig. 2. Relationships between the occurrence of different prey groups (mammals, fish and birds) in the diet of female American mink ($n = 9$) in the Archipelago Sea, SW Finland, in summers 2004–2005 and (a) home-range size (land area, ha), (b) mean distance between islands within home-range boundaries, and (c) the number of islands within 1 km radius outside home-range boundaries.

cantly different relationships of home-range size to the three main prey groups (Wilks' $\lambda = 0.25$,

$F_{2,5} = 7.34$, $P = 0.033$), whereby the occurrence of mammals in the diet increased with home-range size. The association with the number of islands within 1 km radius was only marginally different between the three prey groups (Wilks' $\lambda = 0.32$, $F_{2,5} = 5.23$, $P = 0.060$).

Discussion

The summer diet of mink in the outer archipelago consisted mainly of fish (33% occurrence in scats), birds (28% occurrence) and mammals (15% occurrence). Overall in Eurasian studies the main preys of mink are fish (32%) and small mammals (25%) with birds, amphibians and crustaceans supplementing the diet (Jędrzejewska *et al.* 2001), and this also applies for mink living on the Finnish mainland (Tolonen 1982). However, the proportion of fish has been even higher in coastal studies (49%) with birds being the second most important prey (22%) (Jędrzejewska *et al.* 2001). This corresponds well with our findings of fish and bird occurrence in mink scats, and the same proportions also apply to mink prey items found during the study: 46% of them were fish and 38% birds.

In a nearby archipelago area (60–100 km east from our study areas), Niemimaa and Pokki (1990) found 44% occurrence for birds, 34% for fish and 16% for mammals in mink scats during summers 1986–1987. The change in occurrences of birds and fish as mink prey may be indicative of a temporal change in mink diet because of changes in availability of these prey groups (Toivola 2008). For example, the number of common eider breeding pairs in Archipelago Sea area had decreased over 40% between years 1998–2002 (Nordström *et al.* 2002; M. Nordström unpubl. data), while at the same time perch and roach populations increased significantly during the last decade (Ådjers *et al.* 2006). Vole populations in the archipelago are not multianually cyclic but show year-to-year variation, which is mostly dependent on summer rains and their effect on vegetation (Banks *et al.* 2004, Fey 2008). This may cause temporal variation also in mink diet; for example Niemimaa and Pokki (1990) recorded a rapid change in the proportion of mammals in mink diet, when a crash in vole

populations forced mink to prey more on fish. In contrast, in Pulliainen (1984) mink diet consisted almost exclusively of small mammals during their population peak on the Finnish mainland. We have no data on vole populations during our study period, but rainfall in summers 2004 and 2005 was above the average (cumulative rainfall in April–August 2004 271 mm, 2005 310 mm; Finnish Meteorological Institute), indicating that vole populations could have been relatively high.

Amphibians appear to be important food items for mink especially in riverside habitats (Jędrzejewska *et al.* 2001), where they may represent even 43% of the diet (Maran *et al.* 1998). We found no amphibians in our mink scat analysis, and only three amphibian remains were found in the field during the two study summers. Niemimaa and Pokki (1990) also found amphibians in the diet of the archipelago mink, but their occurrence was less than 1%. While amphibians appear to play a minor role in mink diet in the archipelago, mink seem to have a large detrimental effect on common frog populations there (Ahola *et al.* 2006).

We found that the occurrence of mammals (mainly field voles) in female mink diet increased with increasing home-range land area. In addition to year-to-year variation, vole population dynamics in the archipelago appear to be determined by metapopulation processes, namely extinction and colonisation (Pokki 1981, Banks *et al.* 2004, Fey 2008). Both processes are driven by overexploitation (Crone *et al.* 2001), where dispersers leave overgrazed islands for new ones, and therefore ensure the long-term persistence of voles in the region (Pokki 1981, Banks *et al.* 2004). Extinction and colonisation are related to island size and isolation, whereby extinctions are less common on larger and less isolated islands (Pokki 1981). This may explain why the occurrence of voles in mink diet correlates positively with mink home-range size: larger home ranges include larger islands, where vole populations are more persistent (Crone *et al.* 2001).

We also found female mink diet composition to be associated with the mean distance between islands within home-range boundaries and the number of neighbouring islands within 1 km range outside home-range boundaries. Increas-

ing distances between islands in home range (i.e. increasing patchiness of home range) was related to increasing proportions of all three prey groups. Contrary to our hypothesis, decreasing isolation of home range was associated with increasing proportions of fish and decreasing proportions of mammals and birds. However, the relationship between diet composition and isolation was weak and the impact of distance between islands was confounded with a quite strong correlation with home-range size.

A possible source of bias in all diet studies based on scats is scavenging, i.e. the animal has not actually killed the prey identified in its diet. The percentage of occurrence method may over-represent scavenged prey because such prey usually is composed of more undigestible material, i.e. fur and bones (Landa *et al.* 1997). On the other hand, the method also tends to rank small food items higher for the same reason; at least in mammalian prey, the amount of undigestible material per unit biomass increases with decreasing body size (e.g. Weaver 1993). In our case scavenging might be of concern in the case of larger adult waterbirds such as eiders killed by the white-tailed sea eagle, as they represent the largest possible prey in the study area.

Another possible source of bias not usually considered in traditional scat-based diet studies is sex-related bias in the data. There is often no knowledge of the sexes of animals contributing to the diet data, but if the species shows sex-related diet selection, then the sex ratio of the sampled animals becomes important. For example, Birks and Dunstone (1985) found female mink to prey on smaller items (e.g. fish) than males. We know that our dataset from 2004–2005 is heavily female-biased; therefore our results may overestimate the proportion of fish and underestimate the proportion of waterfowl in mink diet as a whole. An adult common eider may be too big a prey for a female mink; however, bird prey in midsummer probably mostly consists of chicks (Niemimaa & Pokki 1990) and therefore the impact of possible bias should be negligible.

The successful invasion of mink in the outer archipelago is probably explained by its opportunistic predation and lack of competitors and predators compared with the mainland. Besides

mink, the only mammalian predators that have managed to settle there permanently are native otters *Lutra lutra*, but they have been extinct from the archipelago for decades (Stjernberg & Hagner-Wahlsten 1994). The main competitor as well as a predator of mink is the white-tailed sea eagle, which also preys mainly on fish and birds (Fischer 1982, Sulkava et al. 1997). However, sea eagles mostly catch pike *Esox lucius* and a wide variety of ducks (Anatidae; Sulkava et al. 1997), and this diet separation probably diminishes the possibility of food competition. On the other hand, sea eagles also prey on small and medium-sized carnivores, including mink and red fox *Vulpes vulpes* (Koivusaari 1980, Sulkava et al. 1997). Because of this intra-guild predation female mink appear to reduce their swimming distances between islands under increasing eagle predation risk (Salo et al. 2008). Another possible competitor to mink is the great cormorant (*Phalacrocorax carbo sinensis*), which preys mainly on viviparous blenny, perch and roach during the breeding season (Lehikoinen 2005). Cormorants are experiencing an explosive population increase along the Finnish coast (from 10 to 12 600 pairs during 1996–2008; Finnish Environment Institute SYKE) and can have strong impact on littoral fish stocks (Rudstam et al. 2004).

Because of their ability to hunt both on land and in water, mink in the archipelago are relying on fish as a sustaining food source year round, which allows mink to have higher impact on other prey (like birds, voles and amphibians) when they become available — a case of apparent competition (Holt 1977). Mink control would be most essential in archipelagos consisting of isolated groups of small islands; such islands serve as refugia for breeding bird colonies but also attract mink. On the mainland, mink face competition and predation from both mammalian and avian predators, and therefore the impact of mink on prey may be more modest.

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