Winter selection of habitats within intertidal foraging areas by mink (*Mustela vison*)

Laura Bonesi*, Nigel Dunstone and Mark O'Connell†

Department of Biological Sciences, University of Durham, Science Laboratories, South Road, Durham DH1 3LE, U.K.

Abstract

Patterns of habitat selection by American mink *Mustela vison* within foraging areas located on the shore, were studied in a coastal environment of Scotland from November to March in 1983/84, 1984/85 and 1994/95. The abundance of prey in the intertidal zone was modelled in relation to abiotic environmental characteristics. Four factors were found to be important predictors of prey abundance: the position within the tidal zone, the abundance and size of rockpools, the nature of the substratum and the presence of fresh water streams. The model was used to predict prey abundance in different areas of the shore. We then investigated whether mink were choosing areas with higher prey abundance at different tidal levels and within, as opposed to between, core areas (areas with a relatively high density of fixes, encompassing usually one or more dens). Only when foraging at low or mid-tide and within core areas were mink found to behave selectively. They showed no significant preference for areas rich in prey when foraging at high tide and between core areas. Mink were also found to avoid areas with fresh water streams and to prefer foraging in the mid-tide zone. The findings are discussed in relation to prey abundance and competition with the otter *Lutra lutra*.

Key words: American mink, *Mustela vison*, habitat selection, interspecific competition

INTRODUCTION

The American mink *Mustela vison*, Schreber is a semi-aquatic mustelid found both in freshwater and marine habitats (Dunstone, 1993). Habitat use by this species, both in coastal and freshwater habitats, has been studied before, and the patterns of space use have been related mainly to the availability and distribution of food and dens, and to disturbance from competitors (Gerell, 1970; Erlinge, 1972; Hatler, 1976; Melquist, Whitman & Hornocker, 1981; Birks & Linn, 1982; Dunstone & Birks, 1985). Most authors have focused on habitat use within the home range of an individual mink. However, an animal's pattern of use of space can be studied at a variety of spatial scales (Wiens, 1989). Ben-David, Bowyer & Faro (1996) studied mink habitat preferences in the summer on the coast of Alaska, and used the foraging sites rather than the entire home range as a sampling unit. In the present study, patterns of habitat selection by feral American mink in winter were investigated at a relatively fine scale, by studying their habitat preferences within intertidal foraging areas. In winter, fish are known to be the major food of both male and female mink in coastal areas (Birks & Dunstone, 1985; Ireland, 1990). Unlike coastal otters *Lutra lutra*, which favour foraging in the open sea (Kruuk, 1995), coastal mink prefer to forage in the intertidal zone when this is not submerged (Dunstone & Birks, 1985). Despite the importance of the intertidal zone as a foraging area in winter, very little is known about the specific use of this habitat by mink in this season.

Radio-tracking studies have shown that the mink uses a number of core areas (typically two to five) within its home range (Dunstone, 1993). Characteristically, mink use one core area intensively for a few days before moving to another (Gerell, 1970). These core areas usually contain one or more dens from which the mink forages in bouts of activity lasting up to 3 h (Bonesi, 1997). Each core area comprises one or more different habitats where the mink can forage, such as woodland, scrub and, on the coast, the intertidal zone (Dunstone, 1993).

In this study we investigated how the mink's selection of foraging areas within the intertidal zone was affected by the state of the tide. Intertidal foraging areas can be located within a given core area or between core areas. Our approach was to model prey abundance within the

* Present address: Department of Zoology, University of Oxford South Parks Road, Oxford OX1 3PS, U.K.
E-mail: laura.bonesi@zoo.ox.ac.uk
† Wildfowl & Wetlands Trust, Slimbridge, Gloucester GL2 7BT, U.K.

intertidal zone, then to use this model to predict prey abundance in different zones of the shore where mink were observed to forage to investigate whether habitat selection was occurring.

METHODS

Study site

Mink were studied on the Ross Peninsula (210 ha), in Dumfries and Galloway region of southern Scotland (grid ref. NX6543). The shore was rocky with numerous shallow rockpools, except for 2 sandy bays. Maximum tidal height was 9 m (range 0.7–9 m). Above the shore, an area of rocks and scrub provided abundant den sites. Otters were present on the Peninsula and spraints were frequently found.

Radio-tracking

Mink were caught with cage traps, anaesthetized with ketamine hydrochloride (11 mg/kg body mass), and fitted with radio-collars weighing 20 g (Biotrack, Wareham, Dorset). The mink studied were all resident individuals, that is they were observed or trapped for all 4 months of the study period. They were located by day and by night using the 'homing-in' method (White & Garrot, 1990). We undertook a formal investigation of the error associated with radio-tracking. In 6 trials involving the location of a hidden radio-collar an error of 9.67 ± 7.17 m ($n = 6$, range 0–20 m) was estimated; 10 times smaller than the average size of the habitat polygons considered. Foraging behaviour was distinguished from travelling on the basis of the speed at which the animal was moving (foraging, range 0–10 m/min; travelling, > 10 m/min).

Two adult males (M1 and M2) and 1 adult female mink (F1), were radio-tracked between November and March in 1983/84, 1984/85 and 1994/95, respectively. Fixes were collected at 5 min intervals for F1 and at 10 min intervals for M1 and M2. Many fixes were collected for each mink to minimize the intra-individual error around the estimate of habitat use. This intensive approach necessarily restricted the number of animals studied.

Prey abundance

We divided the shore (16.6 ha) into 67 habitat polygons (mean size 0.25 ha, range 0.02–0.89 ha), each of which was homogeneous with respect to: substratum (rocks, boulders, shingle and sand), exposure to wave-action (according to Ballantine, 1961), relative abundance of rockpools (none, < 30%, 30–50%, > 50% of the polygon area), size of rockpools (< 1 m², 1–2 m², > 2 m²), presence of fresh water streams, tidal zone (low tide, mid-tide 1, mid-tide 2, high tide). Tidal zones were distinguished by the distribution of algae and invertebrates as described by Lewis (1964).

An index was used to evaluate prey abundance in each polygon. Between December and March, potential prey were sampled using 20, 1-m wide, transects c. 200 m apart. Transect surveys were carried out at low tide and were of variable length, each being located perpendicular to the main direction of the shore between the water-edge and MHWS (mean high water springs). Rockpools were sampled when encountered along the transect ($n = 54$). Only those prey species that are known to occur in the mink's diet in this study area (Dunstone & Birks, 1987) were included in the analysis. Crabs *Carcinus maenas* with a carapace < 3.0 cm wide were excluded from the analysis, as they were not considered to be a significant prey item, since laboratory-based, prey-selection experiments have demonstrated that crabs provide a low ratio of energy content to handling time. Prey abundance was assumed to be constant across the winter. Kruuk, Nolet & French (1988) and Kruuk (1995) have demonstrated this to be valid for 5 of the 7 species of intertidal prey (see Results) known to be taken by mink in this study area. Relative (but not absolute) prey abundance in different habitats was assumed to be the same in different years.

Stepwise multiple regression was used to model the abundance of prey (1) within and (2) outside of the rockpools. The prey abundance index was given by the sum of the 2 equations obtained from the regression analysis. Fish are c. 20% more rewarding in energy content/g than crabs (Watt, 1991 cited by Kruuk, 1995) and have a shorter handling time. A correction weighting, where fish were given a weighting of 2/3 and the crabs a weighting of 1/3, took into account the energy content and the handling time of fish compared with crabs.

Habitat selection

In this study, habitat selection was investigated within foraging areas located on the shore, each of which encompassed several habitat polygons. To assess foraging areas, only radio-tracking fixes from active mink were included. Foraging areas were located within or between core areas of an animal's home range, and were defined as that portion of the shore available between the water-edge and MHWS, and a line perpendicular to the main direction of the shore and passing through the 2 most extreme fixes recorded for the core area. The position of the water-edge varied according to the state of the tide (low, mid- or high tide). Core areas were determined with the 'density circles method' (Bonesi, 1997), based on the relative density of fixes.

Each habitat polygon was assigned to 1 of 3 classes according to its prey abundance score (low, medium and high prey abundance habitats). The null hypothesis, that the use of a particular class occurs in proportion to its availability when all classes are considered simultaneously, was tested with χ^2 goodness-of-fit analysis

Table 1. Sample size from the radio-tracking study and codes of foraging areas identified for each mink *Mustela vison*. Most fixes represent mink in a den

Mink	Total no. of fixes	Travelling fixes	Foraging fixes	Foraging bouts	Days of tracking	Foraging areas
M1	747	18	118	20	26	FA1
M2	906	69	56	12	49	FA2
F1	2641	104	311	45	45	FA3, FA4,FA5

(Neu, Bayers & Peek, 1974). Where the foraging areas of different mink were coincident, data were pooled, as the habitat available was the same. The χ^2 test was applied if the average expected observations over all categories was 6 or more (Roscoe & Bayars, 1971 cited by Neu *et al.*, 1974). Where significant results were obtained, each class was tested with a Bonferroni Z-statistic ($P = 0.1$, Z score = 2.128) to see whether its use diverged significantly from availability (level of significance chosen following Neu *et al.*, 1974).

Time spent in a given habitat (or class), was chosen as a measure of habitat preference (see Charnov, 1976; Parker & Stuart, 1976). The amount of time that the animal spent 'searching' in each habitat, rather than the total amount of time including handling and eating time, was considered. Hence, when the animal was foraging but not moving, only the first fix of the series of consecutive fixes was included in the analysis.

The calculations and statistical analysis were performed with EXCEL 5.0c and SPSS for Windows 6.1.1. Habitat use and availability were calculated with the G.I.S. software Arc/Info (Version 7.0.3, ESRI, Inc. Redlands, U.S.A.).
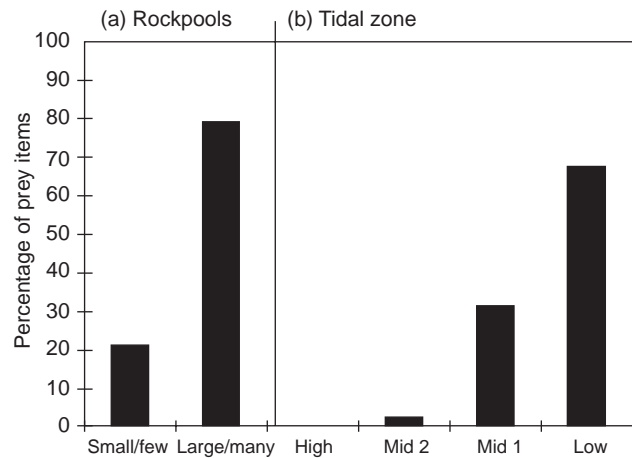
RESULTS

Radio-tracking

Table 1 shows the sample sizes from the radio-tracking study and the number of foraging areas identified for each mink. One foraging area was identified for M1 (FA1), one for M2 (FA2), and three for F1 (FA3, FA4, FA5). The areas FA1, FA2, FA3, FA4 were centred on core areas, and FA5 was located between two core areas. Data for areas FA1 and FA2, belonging respectively to the males M1 and M2, were pooled in the habitat selection analysis since these foraging areas were coincident and the distribution of fixes within each prey abundance class at different tidal levels was similar ($r = 0.60$, $n = 9$ classes). This complete overlap was possible since these two mink occupied the same area in different years.

Shore transects

Seven species of prey were found during the transects: eel *Anguilla anguilla* ($n = 2$), blenny *Lipophyris pholis* ($n = 31$), butterfish *Pholis gunnelus* ($n = 3$), five-bearded rockling *Ciliata mustela* ($n = 3$), seascorpion *Taurulus*

Fig. 1. (a) Percentage of prey items found in areas with different abundance and size of rockpools; (b) percentage of prey items found in rockpools in different tidal zones.

bubalis ($n = 3$), goby *Gobius* spp. ($n = 1$) and shore crab *Carcinus maenas* ($n = 84$). Blennies were the most common fish (67% and 75% of fish captures within and outside of rockpools, respectively). Crabs were also relatively common during the winter season (29% and 43% of total captures within and outside of rockpools). Areas with sand or shingle were poor in terms of potential prey for mink; none of the foraging areas included sandy or shingle bays, therefore these habitats were excluded from further analysis.

Prey abundance

The abundance of prey within rockpools was associated with the abundance and size of rockpools (Fig. 1a) and their position within the tidal zone (ANOVA, $F_{2,61} = 14.78$, $P < 0.001$). Rockpools in the lower shore were much richer in prey suitable for mink than those in the upper shore (Fig. 1b). The presence of freshwater streams and the nature of the substrata determined the abundance of prey outside rockpools (ANOVA, $F_{2,61} = 10.82$, $P < 0.001$). The presence of fresh water had a negative effect on prey abundance, as no prey items suitable for mink were found where fresh water was present (Fig. 2a). The regression also indicated that prey living outside rockpools were more commonly found in areas with boulders rather than bare rock (Fig. 2b).

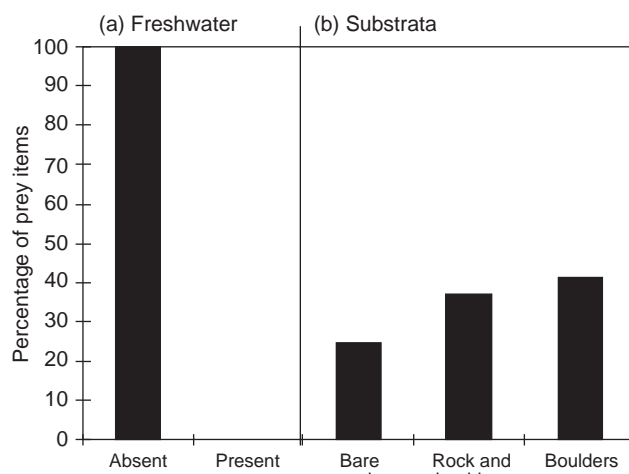The prey abundance index, given by the sum of the

Fig. 2. (a) Percentage of prey items found outside rockpools in areas with or without freshwater streams; (b) percentage of prey items found outside rockpools on different substrata.

two regression equations for prey within (E1 = 2.25 + 2.39 rockpools – 0.85 tidal zone) and outside (E2 = –1.57 – 4.92 fresh water + 2.21 substratum) of pools, was used to assign a score to each polygon based on statistically significant habitat variables in the model. Prey abundance scores ranged from –1.01 to 15.17 (mean 6.92 ± 5.15, n = 67 polygons). Lower scores indicate poor foraging areas. To test habitat selection, the polygons were separated into three classes of equal size (–1.01 to 4.38, 4.39–9.78, 9.79–15.17) according to their prey abundance score. These classes are referred to as 'prey abundance classes'; 21% of the study area falling into the lower class, 26% in the medium class, and 53% in the higher class.

Habitat selection

Mink were recorded foraging both in rockpools and on the shore, but not in the sea. Usually, when foraging at the times of low and mid-tide, mink were selective in their habitat use (Table 2). The exception was for foraging area 5 (FA5), where apparently no selection occurred. This is the only foraging area located between two core areas. When foraging in this area, mink F1 moved faster (mean speed in FA5 = 10.50 ± 1.62 m/min, n = 110) than when foraging within one of the two core areas (FA3 = 7.34 ± 0.66 m/min, n = 183; FA4 = 7.13 ± 0.67 m/min, n = 212) (t = 2.00, d.f. = 27, P < 0.05, one-tail). In two out of three cases the mink were not selective when foraging at high tide (Table 2). The only significant result obtained was for area 4 (FA4), but this was not confirmed when preference/avoidance of each prey abundance class was tested with the Bonferroni Z-statistic. This indicated that all areas within the three prey abundance classes were used in proportion to their availability, suggesting that overall the animals did not forage selectively when foraging at high tide.

To investigate why there was a lack of selectivity at

Table 2. Results of χ^2 goodness-of-fit test for selection of polygons with different prey abundance within each foraging area. Significance: NS, not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. NC = not calculated because too few fixes. Brackets indicate that the significance of the result was not confirmed when preference/avoidance of each prey abundance class was tested with the Bonferroni Z-statistic

Foraging area	Foraging time		
	Low tide	Mid-tide	High tide
FA1/2	**	***	NS
FA3	*	*	NS
FA4	**	**	(**)
FA5	NS	NC	NC

Table 3. Results of Bonferroni Z-statistic for testing avoidance of or preference for each prey abundance class. The signs indicate whether the class has been preferred (+), avoided (–), or used in proportion to its availability (=). Significance: $P = 0.1$, for which Z-score = 2.128 (see Neu et al., 1974)

State of the tide	Foraging area	Prey abundance class		
		Low	Medium	High
Low tide	FA1/2	–	=	+
	FA3	–	=	+
	FA4	–	=	=
Mid-tide	FA1/2	–	–	+
	FA3	–	=	+
	FA4	–	=	=

high tide, the amount of time mink spent foraging on the shore and in the area above the shore were compared. When the tide was low, mink spent most of their foraging time on the shore (M1 = 91%, M2 = 98%, F1 = 97% of fixes), while at high tide they individually reduced the time they spent on the shore (M1 = 82%, M2 = 17%, F1 = 87% of fixes) and increased time spent in the area above MHWS.

Since mink were found to forage selectively at low and mid-tide levels, we tested each prey abundance class separately to see whether it was preferred, avoided or used according to its availability. The results showed that areas with low prey abundance were always avoided (Table 3). Areas with an intermediate prey abundance were mostly used according to their availability and areas with high prey abundance were generally preferred.

Somewhat unexpectedly, mink did not always forage in areas with the highest prey availability. Only rarely were any of the three mink observed to forage in the low tide zone (17% of fixes, range = 5–25, n = 4) despite abundant foraging opportunities. The mink favoured Mid 1, the lower of the two tide areas (55% of fixes, range = 30–86, n = 4), which had about half of the prey items found in the low tide area (Fig. 1b). Apart from this anomaly, mink were observed to forage mainly in areas likely to host the most numerous prey, when foraging at low or mid-tide, that is areas with no fresh

water (81% of total fixes, range = 65–100, $n = 8$), with no sand or shingle (100% of fixes, $n = 8$), and with many rockpools (70% of total fixes, range = 62–91, $n = 8$), and to avoid the high tidal zone (9% of total fixes, range = 0–15, $n = 8$). Mink were recorded foraging both in rocky areas and in boulder fields, and showed no significant preference for either habitat.

DISCUSSION

The results show that the mink we studied did not always prefer areas with high prey abundance and avoid areas with low prey abundance when foraging on the shore, i.e. they did not always behave selectively.

For resident mink, selectivity of particular habitats within a foraging area depended on tidal state. When foraging at low or mid-tide times, mink chose the best areas in terms of prey abundance and avoided areas scarce in prey. When foraging at high tide, however, they were not selective. This is probably because at high tide the only area available was the least productive zone of the shore, and mink spent a greater time in the rock/scrub area and less time foraging on the shore. This apparent link between the low productivity of a habitat and low selectivity by mink might be explained if their use of the shore was conditioned by what prey was available above MHWS. Foraging in two habitats during the same foraging bout might create a searching pattern by which the mink selects primarily the most suitable foraging areas in the rock/scrub area above the shore and only occasionally searches for prey on the shore. Our hypothesis is that foraging on the shore, when only the high tide zone is available, becomes less productive compared to foraging in the rock/scrub area, and this results in a non-selective pattern of foraging.

Another factor that may determine selective behaviour is the motivation for the activity out of den: either the mink was moving about with the primary intention of foraging, or it was moving with the additional intention of reaching a specific place within its home range. For foraging, the activity took place within the same core area, while in the second case the activity led the mink from one core area to another. These different types of movements within the home range have been observed also by Gerell (1970) and Birks & Linn (1982) in riverine habitats. In our study, when a mink travelled between core areas it moved faster, for longer distances, through areas of the shore that it seldom used for foraging, and behaved non-selectively. It is probable that the mink was mainly driven by the necessity to reach its destination as safely and quickly as possible.

Mink were observed to actively avoid the high tidal zone and areas with fresh water streams, confirming the model's prediction of low prey abundance in such areas. The presence of freshwater pools for washing salt water from their fur was found to be an important habitat requirement for otters in Shetland (Kruuk, Moorhouse *et al.*, 1989). It is possible that freshwater pools are also an important requirement for mink. However, the observation of Kruuk, Moorhouse *et al.* (1989) is not in conflict with the findings of the present study, since in this study fresh water was not available in pools, but as a shallow flow on the shore over a relatively large area, and was not suitable for either a mink or an otter to wash its fur in.

Mink were recorded foraging both in rocky areas and in boulder fields, and showed no significant preference for either habitat, but they avoided areas with sand or shingle. Ben-David *et al.* (1996) found a similar result on the coast of Alaska, with mink avoiding shingle and gravel and preferring areas with boulders and bedrock. One of the most common fish prey found on the shore in our study site, the blenny *L. pholis*, is also the most important fish in the diet of mink in this area (Dunstone & Birks, 1987; Ireland, 1990). During a survey of 45 rockpools, Dunstone & Birks (1987) found that the blenny represented only 14% of the total fish found. In the present study, the blenny was found to be the most abundant fish prey both in rockpools (67% of occurrence) and in boulder fields (75% of occurrence). This evidence suggests that boulder fields might be important feeding areas as well as rockpools, whose importance has been stressed in previous studies (Dunstone & Birks, 1987). The mink's poor ability to hunt underwater also supports this hypothesis: Poole & Dunstone (1976) found that mink are not efficient swimmers and their vision underwater is poor, especially in conditions of reduced light (Dunstone & Sinclair, 1978). Hunting in rockpools is also expensive from an energetic point of view, especially in winter, since there is a greater heat loss due to the contact with a wet and cold medium, as shown for the otter by Kruuk, Balharry & Taylor (1994).

The scale at which the selection was investigated yielded interesting results that might be used to make predictions on what occurs at broader scales in coastal areas. The results of this study lead us to predict that mink should live at higher densities in coastal areas with heterogeneous shores providing abundant and large rockpools, boulder fields, a wide mid-tide zone, no freshwater streams, and few or no areas comprising sand and shingle. These findings relate only to foraging during the winter months; in other seasons, there could be different factors influencing habitat preferences by mink.

Apart from food availability and distribution, there are also other important factors that might determine the spatial organization of mink, such as the distribution of den sites and the presence of competitors. Dens are a particularly important requirement when establishing a feeding area, since they might restrict the possibility for a mink to exploit areas rich in food (Gerell, 1970; Birks & Linn, 1982; Halliwell & Macdonald, 1996). Competition with the otter is known to be an important factor in restricting the dispersion of mink in coastal areas where fish are limited and terrestrial prey, such as rabbits, are scarce (Clode & Macdonald, 1995). Competition might be mitigated in heterogeneous environments, which are known to

favour the spatial segregation of competing species (Begon, Harper & Townsend, 1990). Melquist *et al.* (1981) observed spatial segregation within the same habitat between mink and river otters *Lutra canadensis* in rivers. They concluded that mink were foraging in sections of the habitat that were inaccessible to the otter. On the Ross Peninsula, otter signs were frequently found and otters were observed on two occasions. Interference competition between mink and otter was recorded during the course of this study, when an otter was seen to steal a fish from one of the tagged mink. Spatial segregation within the shore might therefore be expected. The results demonstrated that, when foraging at low tide, mink tended to avoid the low tidal zone. Such behaviour could be because either this area is seldom available (being completely uncovered only at low spring tides) or the very low shore is the favourite hunting area of the otter (Kruuk, 1995) and mink might need to avoid direct competition. Melquist *et al.* (1981) have argued that environmental heterogeneity is the major factor in promoting the coexistence of mink and otter in riverine habitats. In coastal areas, the shore is probably one of the most heterogeneous habitats enhancing the coexistence of these two species.

Acknowledgements

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