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# Differential habitat use promotes sustainable coexistence between the specialist otter and the generalist mink

**Laura Bonesi and David W. Macdonald**

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Optimal foraging and habitat selection theories predict that heterogeneous environments should favour the coexistence of competitors, especially when the dominant competitor is a specialist and the sub-ordinate is a generalist. In this paper, we analysed differential habitat use as a potential mechanism for the coexistence of two competing riparian mammals, the specialist and dominant Eurasian otter (*Lutra lutra*) and the generalist and sub-ordinate American mink (*Mustela vison*). We tested three hypotheses: H1: mink coexist with otters for longer in areas with abundance of habitats hosting terrestrial prey because, by not relying on aquatic prey, mink can segregate from its competitor. H2: the characteristics of the habitat closer to the riverbank will affect the length of time the two species coexist, because mink are still tied to the water even in the presence of otters. H3: denser vegetative cover along the bank increases the duration of coexistence of mink and otters because it reduces the frequency of their encounters. The first hypothesis was supported by the data and we found that in areas where terrestrial prey was abundant mink coexisted for longer with otters. The second hypothesis was also supported by the data and the characteristics of the habitat closer to the riverbank were the most important in determining coexistence time. Finally, we did not find supporting evidence for the third hypothesis. This study provides strong evidence that habitat heterogeneity plays an important role in determining the likelihood of coexistence of American mink with Eurasian otters. This result is particularly important from a conservation standpoint. Mink are invasive and a threat to endangered species in parts of their range. The knowledge that mink have a higher chance to persist in the presence of otters when terrestrial prey is abundant should be used to target areas for preferential mink management.

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As discussed in detail by several authors (Levin 1974, Yodzis 1978, Hastings 1980), spatial variations in the environment can promote coexistence. Early theoretical models showed that two species that share resources cannot coexist in a single patch, but they can do so when two or more different patches are present (Levin 1974). In the 1980s the concept that spatial heterogeneity promotes coexistence was explored further in a theory developed to explain species coexistence based on optimal foraging and habitat selection theories, known as the isoleg theory (Pimm and Rosenzweig 1981, Rosenzweig 1981). This theory explains how two competing species distribute themselves in habitats of different quality according to their intra- and inter-specific densities. One of the main predictions of the isoleg theory is that coexistence is favoured when one of the competing species is a specialist behaving selectively, while the other is a generalist behaving opportunistically (Rosenzweig 1987). When the specialist is also the dominant species coexistence is predicted to be favoured in areas with a sufficient diversity of habitats where the sub-ordinate generalist can segregate from the dominant

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specialist. A similar concept was developed earlier for predator–prey systems - prey can seek safety from predators in areas known as predator refuges, which can be crucial for the persistence of both preys and predators (Hassell and May 1973). This principle can equally be applied to interspecific competition and, in a heterogeneous environment, species with low competitive ability can persist by using competition refuges where competition is reduced (Durant 1998).

Knowing about the effect of habitat on species coexistence may be particularly relevant when it may affect conservation and management policies. The present study deals with a species of particular management interest, the American mink. This species has been introduced to England from North America for the fur farming industry. Feral populations of mink were detected in the wild starting from the 1950s (Linn and Stevenson 1980) and since mink colonised most of the British Isles, being now widely distributed (Strachan and Jefferies 1996). The spread of mink has coincided with the demise of the water vole, which, as a consequence of predation by mink, has now become highly endangered (Macdonald and Strachan 1999, Strachan, et al. 2000). In recent years mink have shown a population decline which has been attributed mainly to the negative effects of competition with otters (Bonesi 2002). Because of the detectable effect of otters on mink populations, these species provide a paradigm to test the effect of spatial variations on promoting the coexistence of competing carnivores. In particular, we investigated the effect of habitat heterogeneity and habitat structure on the duration of coexistence of otters and mink and tested three hypotheses.

The first hypothesis states that mink coexist with otters for longer in areas where alternative terrestrial prey is abundant. This hypothesis was prompted by two observations. First, mink have been observed to be excluded from the preferred otter habitat by interference from the otter (Erlinge 1972, Bonesi and Macdonald in press), and, second, as the density of otters grows, the terrestrial portion of the diet of mink increases while the aquatic portion decreases (Clode and Macdonald 1995, Bonesi, et al. in press). Substantial changes in the diet of mink are possible thanks to their generalist dietary habits that allow them to be flexible and exploit both aquatic and terrestrial prey sources (McDonald 2002 for a review). Otters instead specialise almost exclusively on aquatic prey (reviewed by Mason and Macdonald 1986, McDonald 2002). These characteristics of otters and mink feeding ecology were particularly suited to test the theoretical prediction that the coexistence of mink (the sub-ordinate generalist competitor) with otters (the dominant specialised competitor) should be favoured in areas with abundant terrestrial prey that can be exploited by mink but less readily by otters. By relying on terrestrial prey, mink can segregate in a different habitat thereby reducing the chances of aggressive encounters with otters, and also they do not have to count on resources that are depleted by the larger and dominant competitor.

The second hypothesis states that the characteristics of the habitat closer to the bank, rather than those further from the bank, will affect the length of time the two species coexist. This hypothesis originates from the spatial habits of these two species. Because of their specialised feeding on aquatic prey, otters are highly restricted to the water bodies along which they live, and their home ranges develop linearly along these features (Green et al. 1984, Durbin 1998). Mink habitat use is more flexible as a result of their more generalist diet and, although in some habitats they rarely leave the bank side (Yamaguchi, et al. 2003), in others, males in particular are known to move inland several hundred meters (Birks 1981, P. Hersteinsson, pers. com.). The rationale behind our second hypothesis is that mink would move away from the water no further than is necessary to avoid interference by the otter as mink is a semi-aquatic species and it is not known to live independently of water bodies. Therefore we expect the characteristics of the habitat near water bodies to determine how long these species coexist, rather than the characteristics of the habitat further away.

The third hypothesis states that denser vegetative cover along the bank increases the length of the coexistence time of mink and otters. This hypothesis predicts that mink will be displaced sooner in areas with little bankside vegetative cover than in areas with plenty of cover. Some studies have shown that environmental characteristics can mediate the effect of interspecific competition among carnivores (Stander, et al. 1997). In particular, studies on African carnivores have shown that open habitats intensify competitive interactions between species that interact aggressively, such as for example lions and spotted hyenas (Creel et al. 2001). Otters and mink also interact aggressively – otters are known to kill mink (Grigor'ev and Egorov 1969) – and they have been observed stealing food from mink (Bonesi et al. 2000). Moreover, otter and mink live in a linear habitat, where they have to cover huge distances to satisfy their needs. The landscape in England is heavily human-modified and rivers are commonly flanked either by pastures or by arable fields, leaving only a narrow strip of vegetation along the bank. As mink and otters move along the water bodies and do not like venturing into the open (Yamaguchi et al. 2003, L. Bonesi, unpubl.), this landscape configuration forces them to move within this narrow strip of vegetation, thereby subjecting them to a relatively high chance of intra- and interspecific encounters. A similar hypothesis on the effects of linear habitat was formulated to explain the impact of mink predation on the water vole (*Arvicola terrestris*). This is known as the 'tightrope hypothesis' and it predicts that mink and water voles would be more likely to co-exist if they were freed from the linear constraint of a narrow swathe of bankside vegetation that characterises many of the British rivers (Barreto et al. 1998).

## Methods

### Species data

Data from the National Otter Survey of England together with data we collected in 1999 were used to investigate our hypotheses. The National Otter Survey of England is a large-scale and long-term survey repeated at intervals of about seven years and it records both presence and absence of mink and otters at 3,188 sites distributed into alternate 50 × 50 km squares across England (Lenton et al. 1980, Strachan et al. 1990, Strachan and Jefferies 1996). We selected six of these 50 × 50 km squares (Fig. 1) and within these squares a total of 270 sites was chosen at random among those repeatedly surveyed in the National Otter Survey. A site was a 600 m section of the shore of each river, lake, or ocean. Information on the presence and absence of otters and mink at each site was recorded for four periods: 1977–79, 1984–86, 1992–94, and in 1999.

Sites within each square were located along each waterway, coast or lake/reservoir shore, and sites were surveyed by walking 600 m along one bank. Mink and otter were considered to be present if signs such as faeces or footprints were found. From the complete set of 270 sites only sites at which the two species interacted were selected, defined here as sites where during the course of the surveys otters replaced mink or where the two species coexisted for one or more surveys. This sample consisted of 70 sites. Populations of mink were effectively continuous within our study area so that sites could potentially be re-colonised, however sites were independent in terms of individuals. Each site was at least five km from the nearest neighbouring site; therefore each site was likely to host a different mink as a mink home range is on average about three km (Dunstone 1993), making the sites spatially independent. To quantify the degree of coexistence of the two species, the length of time for which mink and otter coexisted was calculated and the data were stratified into three groups:

1) Otters replace mink between one survey and the next and no coexistence is observed. In this case they might have coexisted between surveys for a maximum of seven years or they might not have coexisted at all. We will refer to this category as ‘no coexistence’.
2) Otter and mink coexisted for one survey (7 to14 years).
3) Otter and mink coexisted for two or more surveys (14 to 28 years).

### Prey species data

To test the first hypothesis, we measured the abundance of mink prey. We used an indirect method, i.e. we quantified the amount of habitat available for the mink’s preferred prey as a surrogate for the density of prey (Macdonald et al. 1981). In the case of small mammals,

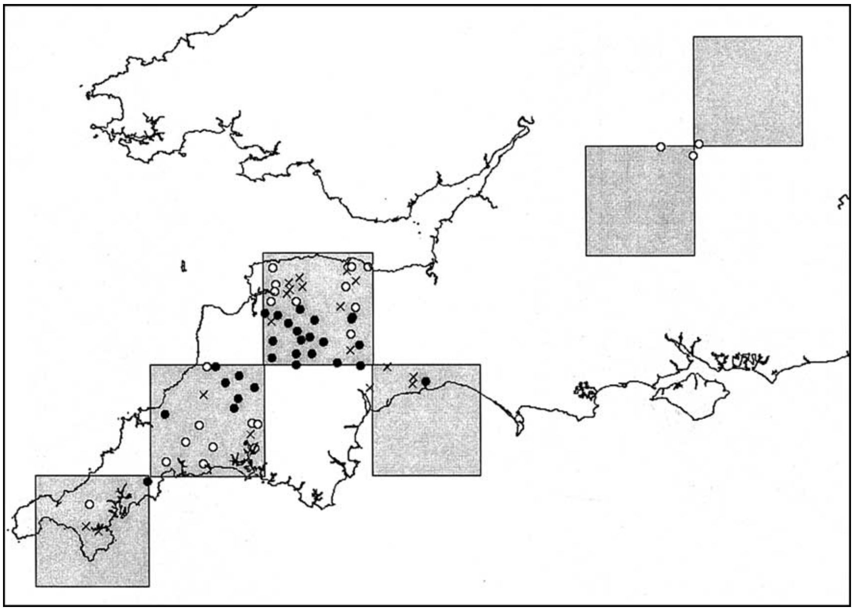

Fig. 1. Location of 50 × 50-km squares in South West England within which sites were surveyed. The points show the location of the sites and indicate the degree of coexistence of mink and otter at each site. An ‘ × ’ indicates no coexistence; an open circle indicates a coexistence of between 7 and 14 years; a close circle indicates a coexistence of 14 to 28 years.

the relationship between habitat and their relative density is well established (Petrusewicz and Hansson 1975). Rabbits (*Oryctolagus cuniculus*) are the main terrestrial prey of mink in England (Day and Linn 1972, Birks and Dunstone 1984) and they are more abundant in scrub (ca 5 rabbits $ha^{-1}$), followed by managed grassland and arable land (ca 2.5 rabbits $ha^{-1}$), and least abundant in woodlands (ca 2 rabbits $ha^{-1}$; Harris et al. 1995; Table 1). Small mammals, such as voles, are also important mink prey and, in general, rough grasslands support a higher density of small mammals than woodlands (Petrusewicz and Hansson 1975; Table 1). Given these considerations, our hypothesis predicts that mink and otters coexist for longer in areas characterised by abundant scrub, managed grassland, and rough grassland and that they coexist for a shorter time in woodlands.

## Habitat data

Two kinds of habitat data were used. Firstly, the data we collected at the 270 selected sites during the 1999 survey. These data were collected using the sampling method of the River Habitat Survey (Raven et al. 1997). The habitat was sampled along 500 m of each 600 m site. Each 500 m stretch was divided into 10 sections of 50 m. Within each 50 m section the dominant (prevalent) habitat was recorded and the complexity of the vegetation along the bank was classified (Table 2). Information on the dominant habitat was recorded at two scales: within 5 m of the banktop and within 50 m from the banktop. The second kind of habitat data was derived from the Institute of Terrestrial Ecology Land Cover Map of 1990–93 aggregated to the 1km square level (Fuller et al. 1994). From the Land Cover data-set we selected the 1 km squares surrounding each of our sampled sites. We refer to the River Habitat Survey 5 m, River Habitat survey 50 m, and Land Cover data as to three different data-sets, and from now on we will abbreviate them as RH5m, RH50m, and LC.

We assumed that no substantial habitat changes occurred between the first survey of 1977–79 and the last survey of 1999. To support this assumption we compared habitat data recorded during the National Otter Survey in 1977–99 with the habitat data we recorded in 1999 at the same sites within 5 m of the bank. In 1977–79 habitats were recorded just as present or absent within the section, while in 1999 habitats were recorded as the percentage of the total length of the section they occupied. We compared each habitat at these two moments in time under the hypothesis that, if the habitat did not substantially change, sites where it was present in 1977–79 should have a significantly higher percentage of that habitat also in 1999 compared to sites where that habitat was recorded absent in 1977–79.

## Spatial scales

To test the first two hypotheses, the duration of coexistence of otter and mink in different habitats was examined at three different spatial scales (Fig. 2a): (i) within 5 m of the banktop; (ii) within 50 m of the banktop; (iii) within the 1 km square surrounding the site. These spatial scales correspond to the three different data-sets RH5m, RH50m, and LC, and they allow us to quantify distinctions predicted from the observation that while both mink and otter prefer to remain very close to the river bank, mink can move hundreds of meters inland (Birks 1981).

To test the third hypothesis, the vegetative cover along the bank was considered, where the bank is defined as that area between the river and the banktop (Fig. 2b). This area was chosen because it is along this feature that mink and otters travel as observed during radio-tracking studies of both species (Yamaguchi et al. 2003, L. Bonesi, unpubl.).

## Analysis

The first step of the analysis consisted of choosing a set of relevant habitat variables. Habitat variables that occurred at a very low frequency ($<4\%$ RH5m and RH50m; $<2$ ha LC) were excluded from the three data sets while all the others were included.

To test the first hypothesis, each of the three spatial scales (5 m, 50 m, 1 $km^2$) was considered separately. The

Table 1. Ranked habitat preferences of the main mammalian prey of mink. Ranks range between 1 = preferred habitat and 3 = least preferred habitat.

| | Scrub | Grassland | Woodland | Source |
|---|---|---|---|---|
| Rabbit (*Oryctolagus cuniculus*) | 1 | 2 | 3 | 2 |
| Bank vole (*Clethrionomys glareolus*) | 1 | 3 | 2 | 1,3,4 |
| Field vole (*Microtus agrestis*) | 2 | 1 | 2 | 1,3 |
| Woodmouse (*Apodemus sylvaticus*) | 1 | 2 | 1 | 1,3,4 |

1 Corbet and Harris (1991).
2 Harris et al. (1995).
3 Newson (1963).
4 Southern and Lowe (1968).

Table 2. Habitat variables initially considered in the analysis. RHS stands for 'River habitat survey'.

| Data set | Category | Variables | Description |
|---|---|---|---|
| RHS | Bank vegetative cover | 1. Bare earth/rock etc.<br>2. Uniform – predominantly one type of vegetation but no scrub or trees<br>3. Simple – two or three vegetation types<br>4. Complex – four or more vegetation types | Vegetative cover on the bank defined on the base of the composition of the vegetation where five types are distinguished: bryophytes, short herbs, tall herbs, scrub, and trees |
| RHS | Land use within 5 m and 50 m of the banktop (RH5m and RH50m) | 1. Broadleaf woodland<br>2. Conifer woodland<br>3. Marshland<br>4. Scrub<br>5. Rough grassland<br>6. Wetland<br>7. Managed grassland<br>8. Tilled land<br>9. Urban/suburban<br>10. Open water | The same habitat variables were measured within 5 and 50 m of the banktop. Within each 50 m section along the bank the dominant habitat only was recorded. |
| Land cover | Land use within 1 km square around the site | 1. Broadleaf woodland<br>2. Conifer woodland<br>3. Rough grassland<br>4. Managed grassland<br>5. Tilled<br>6. Open shrub }<br>7. Dense shrub }<br>8. Heath }<br>9. Urban/suburban<br>10. Bracken<br>11. Bog | These were merged into a single variable called 'scrub' |

extent of each habitat was quantified by calculating the percentage of 50 m sections with that specific habitat type within each 500 m site (RH5m and RH50m), and by calculating the number of ha with that specific habitat type in each 1 km square (LC). Percentages were arcsine transformed for normality (Zar 1996). Because habitat variables were likely to be correlated, principal component analysis was used to summarise them (Tabachnick and Fidell 1989). With this method variables that are correlated with one another, but largely independent of other sub-sets of variables, are combined into fewer components. The resulting components were tested for normality using a Kolmogorov-Smirnov normality test and for homogeneity of variances using Bartlett's test

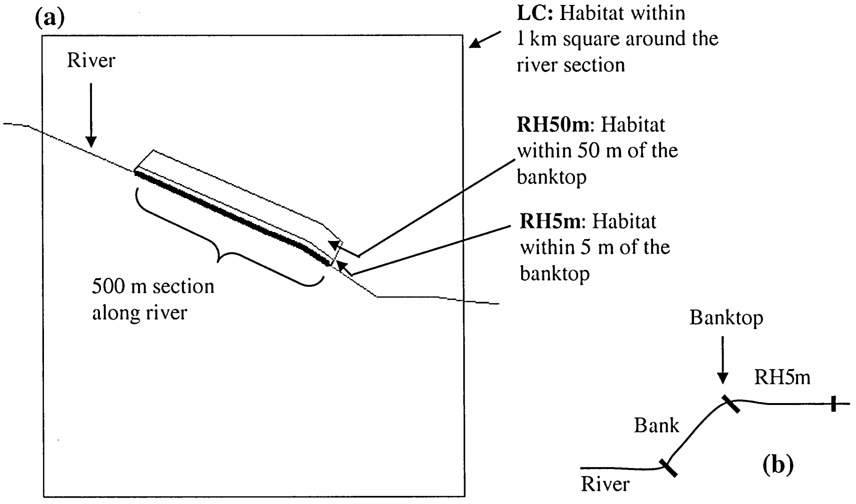

Fig. 2. (a) Schematic representation of the spatial scales considered to test the first two hypotheses; (b) location of the bank, defined as that area between the river and the banktop.

(Zar 1996). Following the results of these tests it was decided to use non-parametric analysis of variance by means of Kruskal-Wallis tests (Zar 1996).

The relationship between otter densities and habitat at all three spatial scales was also investigated to exclude the possibility that the patterns observed were due to the density of otters rather than to the effect of habitat. As a crude measure of otter relative densities the number of spraints in a given section was used (Conroy and French 1987, Mason and Macdonald 1987, Strachan and Jefferies 1996). The Bonferroni adjustment for multiple tests was used to take into account that two correlations were carried out for RH5m and RH50m (Zar 1996), lowering the level at which a result would be accepted as significant from 0.050 to 0.025 ( = 0.050/2 tests).

To test the second hypothesis, the significance of the results at the three spatial scales was compared, predicting that only the most relevant spatial scales would give significant results.

For the third hypothesis, we used the same approach as for the first one, and tested whether the duration of coexistence varied with the extent of vegetative cover on the bank, expecting that a higher percentage of cover would promote coexistence. The extent of vegetative cover was quantified by calculating the percentage of 50 m sections with complex cover within the 500 m site (Table 2 for a definition of cover).

## Results

### Testing the assumption

The assumption that habitat did not substantially change between 1977–79 and 1999 was supported by the data. Of the three habitat variables that were collected both in 1977–79 and 1999, woodland, managed grassland and tilled land, we were able to test only broadleaf woodland because the other two were respectively too frequent or too rare to be tested. However, given that these three variables are expected to be correlated (below) testing only one was probably sufficient to support our assumption. Sections where broadleaf woodland was recorded present in 1977–79 had on average 62% (SD = 5.8, n = 32) of woodland in 1999, while sections where broadleaf woodland was recorded absent in 1977–79 had on average only 21% (SD = 5.5, n = 36) of woodland in 1999 (t-test = 5.2, df = 66, p < 0.001). However, the fact that habitat in 1977–79 correlated with that in 1999 does not exclude that some changes did occur, but they were not large enough to alter substantially habitat composition.

### H1: mink coexist with otters for longer in areas where terrestrial prey is abundant

*Selection of habitat variables*

The following variables from the RH5 m and RH50 m were included in the analysis: 'managed grassland', 'rough grassland', 'tilled land', 'broadleaf woodland', and 'scrub', because they were the dominant habitat in at least 4% of cases**.** The variables 'conifer woodland', 'marshland', 'urban/suburban', 'wetland', and 'open water' were excluded from the RH5 m and RH50 m because they occurred at a very low frequency.

From the LC data-set the following variables were excluded: 'urban/suburban', 'bracken', 'bog', and 'coniferous woodland' because these habitat types occurred at a very low frequency. 'Managed grassland', 'rough grassland, 'scrub', 'broadleaf woodland', and 'tilled' were instead included.

When examining whether variables were correlated between data-sets, it was found that all dominant habitats within 5 m of the bank correlated with those within 50 m of the bank in the RH surveys (Table 3). Dominant habitats within 50 m of the bank in the RH survey correlated with LC habitats in most cases (Table 3), with the exception of rough grassland (Pearson correlation coefficient = 0.15, df = 68, p = 0.220), and broadleaf woodland (Pearson correlation coefficient = 0.18, df = 68, p = 0.143).

*Principal components analysis*

We summarised the above habitat variables into fewer components using principal components analysis. Only components with eigenvalues greater than one were retained. Two components were extracted for each

Table 3. Significant correlations between habitat variables of different data sets. The arrows indicate a positive significant correlation between two variables ($p < 0.05$). Habitat for RH5 m and RH50 m was measured as the percentage of 50 m sections within each 500 m site where that particular habitat was dominant. Habitat for land cover is expressed as the number of ha of a specific habitat per 1 km square.

| RHS5m | | RHS50m | | Land cover |
|---|---|---|---|---|
| | | Tilled | ↔ | Tilled |
| Managed grassland | ↔ | Managed grassland | ↔ | Managed grassland |
| Rough grassland | ↔ | Rough grassland | | Rough grassland |
| Broadleaf wood | ↔ | Broadleaf wood | ↗<br>↘ | Broadleaf wood |
| Scrub | ↔ | Scrub | | |
| | | | | Scrub |

data-set explaining 76%, 62%, and 68% of the variance in RH5m, RH50m and LC respectively. The results of PCA are shown in Table 4. In RH5m, the first component accounts for sections characterised by woodland, while the second component is characterised by sections with managed grassland. In RH50m, the first component accounts for sections characterised by managed grassland and scarce woodland, the second for sections characterised by woodland and little rough grassland and scrub. In LC, the first component is characterised by managed grassland and scarce woodland and rough grassland, while the second is characterised by tilled land.

### *Analysis of variance*

There were 19 sites where mink and otters did not coexist, 23 sites where they coexisted for one survey, and 28 sites where they coexisted for two or more surveys (Fig. 1). The results of Kruskal-Wallis tests in Table 5 show that only component 2 of RH50m was significant, and that component 1 of RH5m was close to significance. When the duration of mink and otter coexistence associated with these two components was analysed more in detail with a Tukey test, it emerged that there was a significant difference of habitat types between sites where otter and mink did not coexist and sites where they coexisted for 14–28 years (Table 6). The graphical analysis of each habitat separately at the 5 m and 50 m scales (Fig. 3, 4) shows that otter and mink tended to coexist for longer when scrub was most abundant, and tended to coexist for shorter times when there were high levels of broadleaf woodland.

If otters were found to live at higher densities in broadleaf woodland and at lower densities in scrub, then the density of otters rather than the type of habitat could be an alternative explanation for the duration of mink and otter coexistence. This possibility was examined by correlating an estimate of the density of otters with the habitat characteristics of the site. Correlations were calculated separately for each of the four surveys (1977–79, 1984–86, 1992–94, and 1999). Only one of the 24 correlations between estimated otter density and habitat types was significant. In 1999, otters were found to live at higher densities when surrounded by woodland (Table 6), but this correlation was relative to the habitat within the 1 km square surrounding the section and no significant correlations were found between otter densities and the habitat closer to the bank.

Table 5. Results of the Kruskal-Wallis test for all three spatial scales represented by the three data-sets RH5m, RH50m and LC. The tests were adjusted for ties. The Kruskal-Wallis statistic is represented by ‘H’; ‘df’ stands for degrees of freedom; ‘p’ is the probability level.

| Data-set | Variable | H | df | p |
|---|---|---|---|---|
| RH5m | PC1 | 4.90 | 2 | 0.086 |
| | PC2 | 1.80 | 2 | 0.407 |
| RH50m | PC1 | 0.82 | 2 | 0.665 |
| | PC2 | 8.03 | 2 | 0.018 |
| LC | PC1 | 1.96 | 2 | 0.376 |
| | PC2 | 2.22 | 2 | 0.330 |

## H2: habitat close to the river is most important for coexistence

The hypothesis that the habitat composition closer to the river is most important in determining the degree of coexistence was supported by the data. Significant habitat differences were found only within 5 and 50 m of the bank, while habitat composition within the 1 km square surrounding the site seemed to have no effect on the duration of coexistence of otters and mink (Table 5, Fig. 5 ).

## H3: a dense bank cover favours coexistence

There was no statistically significant difference in the duration of coexistence between otter and mink depending on the amount of vegetative cover on the bank. There was, however, a tendency for vegetative

Table 4. Results of the principal component analysis for the three data-sets RH5m, RH50m and LC. Correlations between the principal components and the habitat variables are shown in the lower table.

| | RH5m | | RH50m | | LC | |
|---|---|---|---|---|---|---|
| | PC1 | PC2 | PC1 | PC2 | PC1 | PC2 |
| Eigenvalue | 1.76 | 1.27 | 1.67 | 1.41 | 1.53 | 1.19 |
| Proportion | 0.44 | 0.32 | 0.33 | 0.28 | 0.38 | 0.30 |
| Cumulative | 0.44 | 0.76 | 0.33 | 0.62 | 0.38 | 0.68 |
| Variable | | | | | | |
| Managed grassland | – 0.33 | 0.78 | 0.73 | 0.01 | 0.68 | – 0.25 |
| Broadleaf woodland | 0.72 | – 0.14 | – 0.47 | 0.58 | – 0.55 | – 0.24 |
| Scrub | – 0.47 | – 0.46 | – 0.16 | – 0.53 | – | – |
| Rough grassland | – 0.38 | – 0.38 | – 0.29 | – 0.62 | – 0.45 | – 0.48 |
| Tilled land | – | – | – 0.37 | – 0.01 | – 0.22 | 0.81 |

Table 6. Results of the Tukey test for differences in the means of the principal components when comparing different levels of coexistence. Levels of coexistence are 1 = no coexistence; 2 = coexistence between 7 and 14 years; 3 = coexistence between 14 and 28 years. The test statistic of the Tukey test is indicated with q. For 67 degrees of freedom, three levels, and a probability of 0.05 the tabulated value of q is 3.40.

| Data-set and variable | Levels tested | q | p |
|---|---|---|---|
| RH5m – PC1 | 1 vs 2 | 1.51 | ns |
| | 2 vs 3 | 1.92 | ns |
| | 1 vs 3 | 3.40 | * |
| RH50m – PC2 | 1 vs 2 | 2.36 | ns |
| | 2 vs 3 | 1.64 | ns |
| | 1 vs 3 | 4.01 | * |

cover to be more abundant at sites where mink and otters coexisted for at least one survey (Fig. 6 – Kruskal-Wallis test: $H = 1.53$; $df = 2$; $p = 0.465$ adjusted for ties). Vegetative cover did correlate negatively with managed grassland (Pearson correlation coefficient = $-0.30$, $p = 0.012$, $n = 70$) and positively with broadleaf woodland (Pearson correlation coefficient = 0.26, $p = 0.028$, $n = 70$), but not with scrub or rough grassland as measured within 5 m from the banktop.

## Discussion

This study supported the prediction that, when a sub-ordinate generalist is sympatric with a dominant specialist, coexistence is favoured in areas that host habitats where the sub-ordinate can segregate from the dominant (Levin 1974, Rosenzweig 1981). We found that mink coexisted for longer with otters in areas characterised by plenty of scrub where mammalian prey, such as rabbits and voles, are particularly abundant. While mink tended to be out-competed rapidly by otters in areas characterised by fewer mammalian prey, where broadleaf woodlands were the dominant habitat. Studies of the diet of mink support these findings and have shown that mink actively change their diet in response to increasing densities of otters (Clode and Macdonald 1995, Bonesi, et al. in press). These studies observed that, as the density of otters increased, the diet of mink shifted toward terrestrial prey and consisted of a higher proportion of mammals and birds while fewer fish and crustaceans were present. The present study, together with the studies on changes in the diet of mink, suggests a general process for the coexistence of mink with otters. In the absence of otters, mink adopt their preferred diet characterised by a relatively high proportion of aquatic prey. As the density of otters increases, mink are forced to shift their diet toward terrestrial prey, but where such prey are scarce mink enter into direct conflict with the otter and, because mink are sub-ordinate competitors, the conflict results in mink having to abandon the area or being killed. The persistence of mink is therefore strongly determined by a complex interaction between mink, otters, and habitat. If our interpretation of the process underlying mink persistence is correct, in the long-term, as the otter

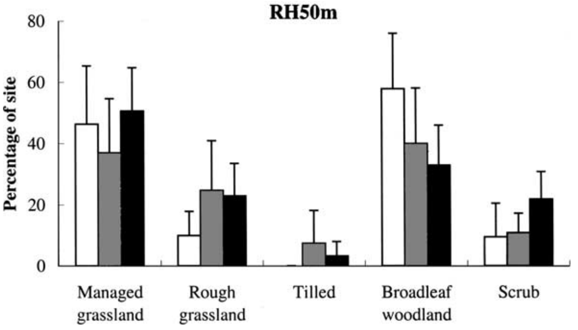

Fig. 4. Average percentage of each habitat type in sites characterised by no, short or long coexistence between mink and otter. Habitat was measured during the 1999 river habitat survey as the prevalent habitat within 50 m from the bank. The bars represent the 95% confidence limits of the mean. Legend as in Fig. 3.

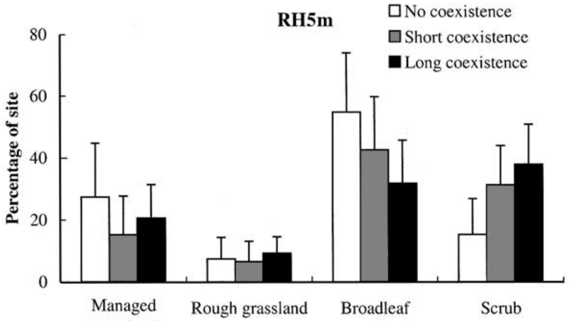

Fig. 3. Average percentage of each habitat type in sites characterised by no, short or long coexistence between mink and otter. Habitat was measured during the 1999 river habitat survey as the prevalent habitat within 5 m from the bank. The bars represent the 95% confidence limits of the mean.

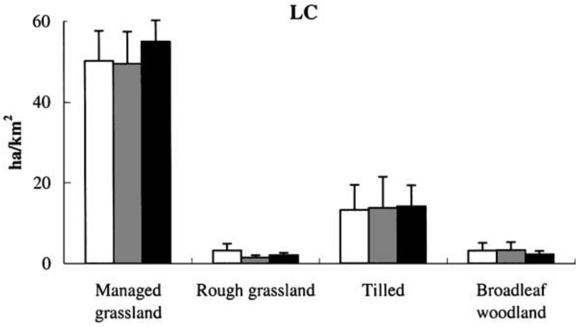

Fig. 5. Average number of hectares of each habitat type in sites characterised by no, short or long coexistence between mink and otter. Habitat was extracted from the land cover data-set and represents the amount of habitat expressed in ha in the 1 km square surrounding the site. The bars represent the 95% confidence limits of the mean. Legend as in Fig. 3.

Table 7. Results of the correlation (Spearman's rank correlation coefficients) between the number of otter spraints, used as an indication of otter densities, and habitat type. Correlations are reported for all four different surveys between 1977 and 1999. One asterisk represents significance at the 0.05 level. The sample size is n = 70 sites.

| Year | Habitat type | RH5m | RH50m | Land cover |
|---|---|---|---|---|
| 1977–79 | Broadleaf woodland | 0.02 | 0.08 | – 0.00 |
| 1977–79 | Scrub | – 0.03 | 0.16 | – |
| 1984–86 | Broadleaf woodland | – 0.16 | – 0.21 | – 0.02 |
| 1984–86 | Scrub | 0.03 | 0.19 | – |
| 1992–94 | Broadleaf woodland | – 0.16 | – 0.14 | 0.01 |
| 1992–94 | Scrub | 0.14 | 0.23 | – |
| 1999 | Broadleaf woodland | 0.07 | 0.04 | 0.26 * |
| 1999 | Scrub | – 0.01 | 0.00 | – |

re-colonises its lost range in the UK (Strachan and Jefferies 1996), we expect mink to disappear from those areas that host little terrestrial prey and to persist in those areas where such prey is abundant.

One of the other carnivores that is most likely to compete with mink in England is the polecat (*Mustela putorius*). There were no established populations of polecats in our study areas (Birks and Kitchener 1999), but it is possible that where polecats are present they may create further problems for the mink by competing with them for terrestrial prey.

One of the predictions of the first hypothesis was that otter and mink should coexist for longer in areas with abundant managed grassland, but this habitat had no effect on coexistence time in spite of being one of the most favourite foraging grounds for rabbits (Thompson and King 1994). Managed grassland was one of the most abundant habitats at the 50 m and 1 km scales, and often more than 50% of the sections had this as their dominant habitat. It is therefore possible that this habitat was sufficiently abundant, i.e. covered a sufficient area, for rabbits to forage and that rabbits were limited more by den sites rather than by food, as some studies suggest (Trout and Smith 1995). Another reason that might explain why managed grassland was not important in determining the duration of coexistence, is that mink hunt rabbits mainly in their warrens (Dunstone 1993), which are located in scrub or hedges more often than in open fields (Kolb 1991). For this reason managed grassland may have little value to the mink as a hunting ground.

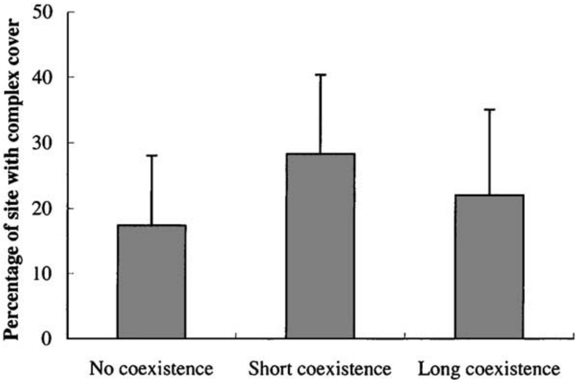

Fig. 6. Percentage of complex vegetation on the bank for different duration of otter and mink coexistence. The bars represent the 95% confidence limits of the mean.

From previous studies it is known that the density of otters is an important factor in determining the length of time mink and otter coexist and that there is an inverse correlation between the density of otters and that of mink (Erlinge 1972, Bonesi and Macdonald in press). These observations are not at odds with the findings of the present paper. We found a weak indication that otters tended to live at higher densities in areas with abundant broadleaf woodland and rough grassland within the 1 km square surrounding the site. However, at the scales of 5 and 50 m at which habitat affected the duration of coexistence, there was no correlation between habitat and the density of otters (Table 7). Moreover, the amount of broadleaf woodland at the 1 km scale was not correlated to broadleaf woodland within 5 and 50 m of the bank (Table 3). We therefore suggest that the patterns observed whereby mink and otter coexisted for longer in areas with abundant scrub and little broadleaf woodland, reflected the fact that areas with scrub hosted more alternative prey for the mink and not that this particular habitat was characterised by higher otter densities in comparison to woodlands.

The results of the second hypothesis illustrated how the choice of an appropriate spatial resolution was important to determine the factors that affect coexistence. The duration of coexistence of otters and mink was determined by the characteristics of the habitat within 5 and 50 m of the bank, while habitat considered at the larger scale of 1 km had no effect. It could be argued that habitat at the 1 km scale was not important because the data used to detect the presence of mink and otter in this study were collected along the riverbank, and therefore if mink were present inland this would not have been detected. However, mink are consistently detected through the presence of signs along the river even when they are sympatric with the otter and when their diet is predominantly terrestrial (Bonesi and Macdonald 2003, Bonesi, et al. in press). Therefore we suggest that the phenomenon observed here – the importance of the characteristics of the habitat close to the river in determining coexistence – underlies a true ecological pattern rather than a bias in the sampling. This pattern could be expected because, even in the presence of otters, mink do not become exclusively terrestrial, but are always tied to the water (Chanin 1976, Birks 1981). This is especially true for females, which appear to be more reliant on aquatic prey (Sealander 1943, Birks and Dunstone 1985).

We found no evidence in support of the third hypothesis, which predicted that mink and otter would coexist longer in areas with plenty of vegetative cover along the bank. Ecologically this may be explained by the fact that otters can detect mink through olfactory cues, in addition to visual ones, therefore cover may not be an obstacle to mink detection.

## Conclusions

In this paper, we showed that otter and mink coexist for longer in habitats where mink can find alternative terrestrial prey, in particular rabbits and voles. The ecological flexibility of mink to exploit terrestrial, as well as aquatic prey is a key factor for its persistence in England despite intense competition by the otter. The knowledge that mink, when sympatric with otters, persist for longer in the presence of abundant terrestrial prey is important for managing mink populations. Mink are an invasive species in the UK and a threat to the endangered water vole (Woodroffe et al. 1990, Macdonald and Strachan 1999). In recent years it has become obvious that in many areas active mink control is the only possible strategy to promote the conservation of the water vole (DoE 1995, Macdonald and Strachan 1999). The results of our study suggest that the interaction of otters and mink and the availability of alternative prey are both factors that should be taken into account when planning mink control. As a possible strategy we suggest that mink control should preferentially be targeted in areas where mink is sympatric with otters and where there is scarcity of alternative terrestrial prey. In areas with these characteristics, control operations are more likely to be successful because of the additive effects of otters on suppressing the density of mink. In evaluating this scenario, it would be important to know whether the residual population density of mink, following the results of competition from otters, was nonetheless sufficiently high to thwart attempts to restore water vole populations.

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