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Competition between Eurasian otter *Lutra lutra* and American mink *Mustela vison* probed by niche shift

Laura Bonesi, Paul Chanin and David W. Macdonald

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Interspecific competition is one of several constraints that might prevent an individual from maximising its energy intake. When an interspecific competitor is introduced, an individual is often forced to shift its diet according to the intensity of the competitive pressure. In this paper, we explore whether the introduced American mink (*Mustela vison* Schreber) shifts its diet when the density of its potential competitor, the Eurasian otter (*Lutra lutra* L.), is increased. We compared the diets of otter and mink at the same location but at two moments in time when the relative densities of these two species were different while controlling for the abundance of aquatic prey. Mink and otters are semi-aquatic mammals belonging to the same guild of mustelids and otters are expected to be the dominant competitor because they are larger and better at hunting underwater. The diets of otters and mink overlap to a great extent but while otters specialise mainly on aquatic prey, mink are able to exploit both aquatic and terrestrial prey. These observations prompted the hypothesis investigated in this work that at higher otter densities the diet of mink should change to include a higher proportion of terrestrial items. This hypothesis was supported by the data and at higher otter densities mink diet was observed to consist of a higher proportion of mammals and birds while fewer fish were present, although this pattern was present only in winter while no changes were observed in spring. Meanwhile the diet of otters remained basically unchanged. In the second part of the study, we investigated whether niche breadth and niche overlap between otter and mink changed at different otter densities. We found that niche overlap declined as the density of otters increased, in agreement with the prediction of habitat selection theory.

L. Bonesi and D. W. Macdonald, Wildlife Conservation Research Unit, Univ. of Oxford, South Parks Road, Oxford, UK, OX1 3PS (laura.bonesi@zoo.ox.ac.uk). – P. Chanin, North View Cottage, Union Road, Crediton, Devon, UK, EX17 3AL.

The two essential prerequisites for the existence of interspecific competition, according to one of the most common definitions of competition (Keddy 2001), are: (i) the competing species must overlap in their use of resources; (ii) the use of the resource by one species (exploitation) or non-consumptive pre-emption of the resource (interference) must reduce resource availability to the other species (Wiens 1989). By assuming that the species compete for food we discuss competition within the context of optimal foraging theory (MacArthur and Pianka 1966, Pyke et al. 1977, Krebs 1978). According to this theory, in the absence of competition an individual is expected to maximise its energy gain given the availability of local resources. When local resources are kept constant and a competitor species is introduced, then one or both competitors are expected to shift their diet according to the intensity of the competitive pressure. If competition is highly asymmetrical then the sub-ordinate competitor is expected to adapt to the dominant one, but little or

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no change is expected in the diet of the dominant competitor.

We tested the effects of competition on niche shift in two riparian mustelids – the Eurasian otter and the American mink. Competition between mink and otters is expected to be highly asymmetrical in favour of the otter (Persson 1985) given that the body weight ratio of otter and mink is about 7:1 and otters are better at exploiting the aquatic food source because they can dive for longer and are better swimmers (Dunstone 1979). Otters are fish specialists and more than 80% of their diet consists of fish (Mason and Macdonald 1986, McDonald 2002), while mink are more generalists and their diet includes prey from both aquatic and terrestrial sources in variable proportions (Dunstone 1993). These observations prompted the hypothesis investigated in this work that at higher otter densities the diet of mink becomes more terrestrial, namely contains more items caught on land than in the water, when compared to the diet of mink at low otter densities. We assumed that mink and otters competed for food rather than for dens because: (i) being larger otters are not able to exploit the smaller mink dens although vice versa is possible, and (ii) in largely wooded areas, such as our study site, dens were very unlikely to be a limiting factor (Green et al. 1986).

A number of studies have been carried out that compare the diets of otters and mink in areas where they are sympatric (Jenkins and Harper 1980, Chanin 1981). The dietary overlap of these species has been observed to vary according to habitat and season. When seasons were analysed separately, one study found that dietary overlap was greater in winter than in summer (Erlinge 1972) while another found that dietary overlap was greater in summer than in winter (Jedrzeijewska et al. 2001). It is not possible to conclude whether or not there is competition by comparing niche overlap at different times of the year because food shortage can both increase or decrease the degree of overlap. Niche overlap may decrease if, as food gets scarcer, the two competing species start feeding on different prey, while niche overlap may increase if food scarcity forces the competitors to hunt even more intensely the few remaining species of prey.

Clode and Macdonald (1995) tested specifically for competition between otter and mink. These authors studied the diet of otter and mink in conditions of sympatry and allopatry in a coastal habitat at the same time of year. They hypothesised that, when sympatric, the diets of mink and otter should diverge. They found that this was true, but that, in an area where there was no alternative terrestrial prey, niche shift was not as pronounced as in areas where there was. In addition to the study by Clode and Macdonald (1995) also Erlinge (1972) and Bueno (1996) examined competition between the American mink and the European otter. Bueno (1996) compared mink diet in rivers with and without otters and reported increased frequency of fish and less terrestrial prey in the diet of mink in the river without otters. Erlinge (1972) compared the otters' diet in the absence and presence of mink and found that it was largely unaffected by mink.

Our study is an extension and a complement of previous studies on mink and otter competition. We used a study design similar to that of Clode and Macdonald (1995), but rather than considering sympatric and allopatric populations of mink and otter at the same point in time, we compared populations at the same location but at two different moments in time, when the relative density of these two species were different. In addition, we also quantified the abundance of aquatic prey, a measurement rarely considered in dietary studies of these species, but that is essential to exclude the possibility that the dietary changes observed are due to prey changes rather than to the interaction between the competitors.

Methods

Study area

We compared the diets and densities of mink and otter at two points in time, in the mid-seventies and late nineties, at a single location on the river Teign (Devon, UK). This is the first river in Britain on which introduced American mink are known to have bred in the wild (Linn and Stevenson 1980). We chose the river Teign as a study area because the diet and density of otter and mink were studied there in the 1970s by one of us, Paul Chanin (1976), setting the basis for the comparison. This area comprises a stretch of 12 km of river and 3 km of tributaries (UK grid ref: SX804883 to SX712893). The river Teign is an oligotrophic river with banks lined by extensive broadleaf woodlands and conifer plantations.

Prey abundance

The abundance of Salmonidae, the most common fish family taken by mink and otter, was assessed using electrofishing data collected by the Environment Agency between 1972 and 1999. The sampling technique used only allowed to sample juvenile salmon while it sampled both juvenile and adult brown trout. The fact that only juvenile salmon were sampled, however, does not affect the appropriateness of the estimate because adults are numerically fewer than juveniles, present only at certain times of the year, and because otter and mink tend to feed mostly on the parr stages (Chanin 1981a, Wise et al. 1981). We used data collected at electrofishing stations just upstream of the study area (from SX684877 to SX639844). We selected six stations, averaged the density of fish caught at these stations, and compared them using a t-test.

Mink and otter densities

Relative densities of otters and mink in the study area were inferred by comparing the abundance of their faeces in 1972–73 with that of 1998–99 and by trapping. The sampling effort in the two times periods was different. In 1998–99 the Teign was visited on eight occasions (Dec 90–Jan 99, Feb–Mar 99, Apr 99, Jun 99, Aug 99, Oct 99, Jan 00 and Mar 00) as opposed to 20 in 1972–73. However, in 1998–99 about 25 km of river were surveyed on each occasion (12.5 km on each bank) while in 1972–73 on average about seven km of river were visited on each occasion (Chanin 1976). To overcome the problem of the difference in sampling effort between the two periods, we calibrated the abundance of mink by estimating mink abundance through trapping. The effort in the case of trapping can be more easily compared as the number of trapping nights (number of traps × days of trapping) can be readily compared.

Diet

We collected mink scats and otter spraints between April 1972 and December 1973, and between December 1998 and March 2000. We compared the diets only between December and June, thereby ignoring the data for the rest of the year, because competition is expected to be stronger at this time of year, especially in winter, due to a shortage of prey (Erlinge 1972, Kruuk 1995). On most occasions, mink faeces, called scats, are easy to recognise and to distinguish from those of otter, called spraints. Otter spraints vary in shape but they have a characteristic smell, a sweet-musky odour that can persist for a long time. Mink scats are usually more compact than those of the otter, often appear cork-screwed, and are about 6–8 cm long and about 0.9 cm in diameter. After collection, faeces were washed, passed through a sieve, dried and analysed under the microscope. Fish were identified to family level and some to species level using the key by Conroy et al. (1993). Birds were identified to family level from the characteristic downy barbules of the feathers using the key by Day (1966). Mammals were identified from a combination of hair scale patterns, the hair's medulla form and the medulla structure by using Teerink's (1991) protocol and key.

Diets are expressed as 'frequency of occurrence' and 'relative frequency of occurrence' (Conroy et al. 1993). Frequency of occurrence is obtained by dividing the total number of occurrences of a particular prey item by the number of scats. Relative frequency of occurrence is obtained by dividing the total number of occurrences of a particular prey item by the total number of items found. Resource overlap was calculated using Pianka's adaptation of MacArthur and Levin's formula of niche overlap (Pianka 1973), while niche breadth was calculated using Hurlbert's standardisation of Levin's formula (Hurlbert 1978, Levins 1968).

When testing our hypothesis, to compare the aquatic and terrestrial components of the diet of otters and mink we included only large prey items, namely birds, mammals, and fish, because these are likely to be hunted actively rather than encountered by chance and therefore require a selective behaviour. We excluded amphibians because they are found at the interface between the aquatic and terrestrial habitats. Large prey items can be found associated with smaller prey items such as insects or worms in the same scat, while the presence of large prey items in scats is almost always mutually exclusive. For this reason it is possible to express the data for large prey items as the percentage of scats with aquatic or terrestrial prey items.

Results

Mink and otter densities

Mink were more abundant in the 1970s than in the 1990s, as shown both by trapping and by the number of scats found (Table 1). The higher number of spraints found in the 1990s indicates that otters were instead more abundant in the 1990s than in the 1970s. In the 1970s there were no resident otters in the study area and only transient individuals were present (Chanin 1976). In 1998 to 2000 there was definitively a resident population of otters, which was estimated to be around 3–5 individuals in the whole river that is about 43 km long (Vadim Sidorovich, pers. comm.).

Prey changes between 1970s and 1990s

The most abundant fish in the river both in the 1970s and in the 1990s were salmon (*Salmo salar*) and trout (*Salmo trutta*) (Chanin 1976, Adam Bailey – Environment Agency, pers. comm.). The electrofishing surveys revealed that the abundance of salmon parr

Table 1. Comparison between the 1970s and 1990s of the total number of otter spraints, mink scats, and mink trapped. These values were calculated over the whole year.

	Otter spraints	Mink scats	Ratio of spraints/scats	Mink trapped/100 trap nights
1972–73	253	475	0.53	1.42
1998–99	701	141	4.97	0.66

was similar in 1999 and in 1972 (Fig. 1, t-test = 0.78, df = 10, p = 0.44, two tails).

There was also no significant difference in the abundance of trout between 1999 and 1972 (Fig. 2, t-test = 0.78, df = 10, p = 0.44, two tails).

Other species of fish found during the electrofishing survey in 1999 were eel (*Anguilla anguilla*), stone loach (*Noemachelius barbatula*), minnow (*Phoxinus phoxin*us), bullhead (*Cottus gobio*), and lamprey (*Lampetra* sp.). All these species were also found during earlier fisheries surveys of the 1960s (Bielby 1964), so presumably they were also present in 1972–73. Although present in both periods, eels are known to have declined (Adam Bailey – Environment Agency pers. comm.) following a trend that was common for this species throughout the UK (Knights et al. 2001).

The terrestrial animal life at the river Teign is that typical of woodland, farmland and riverside. No systematic survey was carried out to quantify the abundance of the terrestrial fauna in 1972–73 or in 1998–99, but species composition did not change. Terrestrial fauna included: frogs (*Rana temporaria*), pigeons (*Columbiformes*), passerine birds, woodmice (*Apodemus sylvaticus*), bank voles (*Clethrionomys glareoulus*), field voles (*Microtus agrestis*), grey squirrels (*Sciurus carolinensis*), and brown rats (*Rattus norvegicus*) (Chanin 1976, Chanin and Linn 1980). Rabbits (*Oryctolagus cuniculus*) were not particularly abundant because the area was mostly wooded. They were seen in the fields at the edges of woods in both periods (Chanin and Linn 1980 and pers. obs.).

There were no crayfish on the river Teign and all arthropods consumed by otter and mink were small.

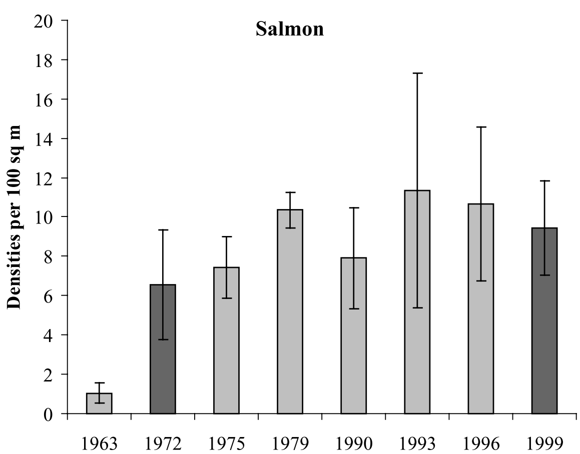

Fig. 1. Densities of salmon parr per 100 m^2 on the river Teign in different years. Data were collected by means of electrofishing at six stations just upstream of the study area. The bars represent ± 1 SE. The darker histogram bars represent the electrofishing surveys contemporary to the data collection on otters and mink.

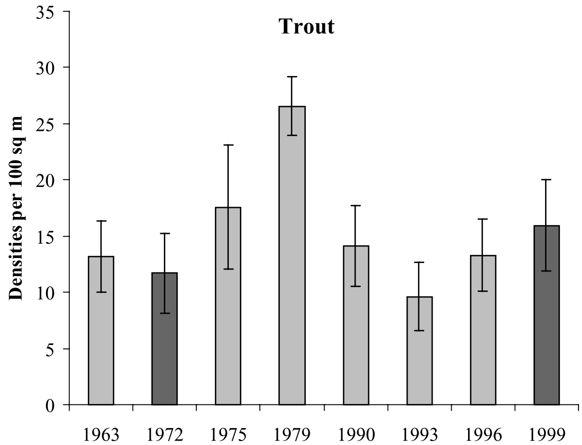

Fig. 2. Densities of trout (parr and adults) per 100 m^2 on the river Teign in different years. Data were collected by means of electrofishing at six stations just upstream of the study area. The bars represent ± 1 SE. The darker histogram bars represent the electrofishing surveys contemporary to the data collection on otters and mink.

Intraspecific comparison of diets: testing the hypothesis

The hypothesis that at higher otter densities the diet of mink shifts toward a more terrestrial based diet was supported by the data (Fig. 3). Between 1972–73 and 1998–99, mink were observed to significantly increase the terrestrial portion of their diet (mammals, and birds) while decreasing the aquatic portion (fish, $\chi^2 = 4.71$, df = 1, p = 0.03). When seasons were analysed separately, it emerged that a significant shift was present in

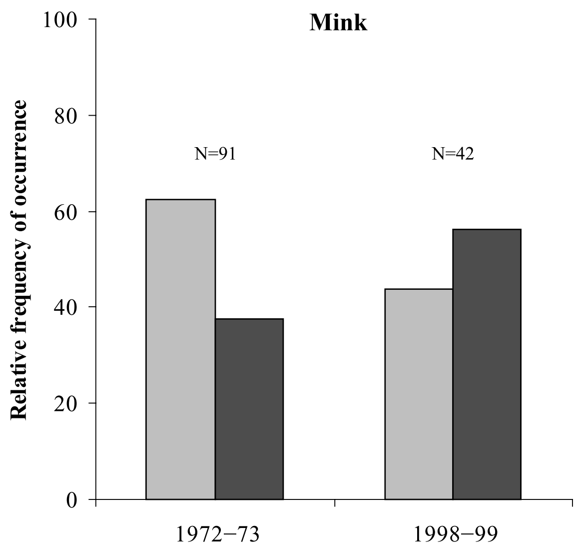

Fig. 3. Relative frequency of occurrence of aquatic (light grey) and terrestrial (dark grey) prey in mink scats in the 1970s and 1990s. Sample sizes are indicated at the top of the histogram bars.

winter ($\chi^2 = 15.7$, df = 1, p $\leq$ 0.001; n = 37 scats in 1972–73 and n = 17 scats in 1998–99) but not in spring ($\chi^2 = 0.1$, df = 1, p = 0.785; n = 54 scats in 1972–73 and n = 25 scats in 1998–99).

The diet of otters remained practically unchanged between the 1970s and 1990s (Fig. 4) and no seasonal differences were present. In otters, there was a slight decrease in the contribution of terrestrial prey items to the diet that was compensated by a greater consumption of amphibians.

Intraspecific comparison of diets: kind of prey taken

The prevalence of different prey items in the diets of otter and of mink changed between 1972–73 and 1998–99 (Table 2). Among mammalian prey, mink increased their consumption of voles and grey squirrels. Fewer species of birds were taken and ralliforms which were absent in 1972–73, started to appear in the diet of mink. Regarding fish species, the consumption of Cottidae increased while that of eels decreased in the diets of both otters and mink. Eels were already thought to be scarce on the Teign in 1972–73 (Chanin 1976), and they declined even further in 1998–99 (Adam Bailey, pers. comm.). Otters were also taking a greater variety of fish species, possibly to compensate for the decrease in eels. Otters and mink increased the consumption of small prey items such as molluscs and arthropods. Weasel hair were found in the faeces of otter and mink in 1972–73 (Chanin 1976) and in one otter spraint in 1998–99.

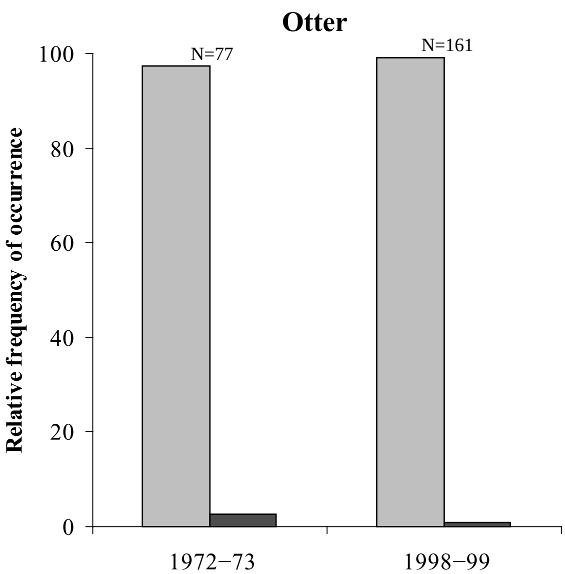

Fig. 4. Relative frequency of occurrence of aquatic (light grey) and terrestrial (dark grey) prey in otter spraints in the 1970s and 1990s. Sample sizes are indicated at the top of the histogram bars.

Niche breadth and niche overlap

Niche breadth increased in both otter and mink between 1972–73 and 1998–99 (Table 3). In 1998–99 otters were taking a greater variety of fish species and both otters and mink took items that were not common in 1972–73 such as arthropods and molluscs. When all prey items were included in the analysis, niche overlap between otter and mink was found to be lower in 1998–99 than in 1972–73 (Table 3). When small items of prey, that are probably not very relevant energetically, were excluded and niche breadth and overlap re-calculated, an even greater decrease in niche overlap was found (Table 3). When seasons were analysed separately, it was found that niche overlap decreased markedly in winter from 0.92 in 1972–73 to 0.23 in 1998–99, while it decreased only slightly in spring from 0.93 to 0.80 (small items of prey excluded).

Discussion

Competition or changes in prey composition?

The results showed that the composition of the diets of both mink and otter changed between the 1970s and the 1990s. In 1998–99 otter and mink consumed more prey items of lower energetic quality, such as arthropods and molluscs. This was probably due to changes in fish composition on the Teign whereby eels, an important prey item in 1972–73, decreased in abundance (Adam Bailey – Environment Agency, pers. comm.). Associated with the decrease in the abundance of eels, otters took a greater variety of alternative fish species, while mink focused their predation on mammals and in particular on voles and squirrels. The necessity to feed on a wider variety of prey items was reflected in the greater niche breadth of both species in the 1990s compared to the 1970s.

Together with an increase in their niche breadth otter and mink showed a decrease in their niche overlap. We argue, based on three observations, that the decrease in their niche overlap was mainly caused by otters forcing mink to shift their diet toward terrestrial prey items. First, mink are known to be able to hunt, and in some areas to rely heavily, on the kind of aquatic preys taken by otters in the 1990s to replace the absence of eels, such as bullhead, minnows, and molluscs (Bueno 1996, Erlinge 1972). In spite of the ability of mink to exploit this kind of prey, they were not a substantial part of the mink diet in the 1990s. Second, while the consumption of terrestrial prey increased in mink, it decreased in otters suggesting that terrestrial prey were not more abundant

Table 2. Comparison of the diets of mink and otter between 1972–73 and 1998–99 (Differences) expressed as differences in frequency of occurrence (FO). A negative value indicates that consumption has decreased between 1972–73 and 1998–99, while a positive value indicates that consumption has increased between these two periods. The last four columns report the frequency of occurrence (FO) and the relative frequency of occurrence (RFO) of prey in mink and otter diets in 1998–99 (Diets in 1998–99). Sample sizes are 42 scats for mink and 161 spraints for otters in 1998–99 and 81 scats and 77 spraints in 1972–73. The category 'Insectivore' comprises moles and shrews.

Category	Differences 70–90s		Diets in 1998–1999			
	FO mink	FO otter	FO mink	FO otter	RFO mink	RFO otter
Insectivore	5	0	7	0	5	0
Lagomorph	– 5	0	5	0	3	0
Bank/field vole	13	0	24	0	16	0
Wood mouse	0.4	– 1	5	0	3	0
Common dormouse	2	0	2	0	2	0
Grey squirrel	7	– 1	7	0	5	0
Rattus	– 1	– 1	0	0	0	0
Unidentified mammal	– 1	1	0	2	0	1
Total mammals					33	1
Anseriform	– 1	0	0	0	0	0
Passeriform	– 4	0	0	0	0	0
Columbiform	– 3	0	0	0	0	0
Galliform	– 3	0	0	0	0	0
Strigiform	– 3	0	0	0	0	0
Ralliform	5	0	5	0	3	0
Unidentified bird	8	0	5	0	6	0
Total birds					9	0
Salmonidae	– 18	– 19	31	66	20	35
Anguillidae	– 10	– 25	7	24	5	13
Stone loach	– 7	– 10	0	1	0	0.3
Cottidae	10	18	10	18	6	10
Minnow	0	3	0	3	0	2
Bullhead	0	1	0	1	0	1
Unidentified fish	1	17	0	17	1	9
Total fish					33	69
Amphibian	– 1	7	2	7	2	4
Earthworm	– 3	– 5	0	0	0	0
Mollusc	2	7	2	7	2	4
Arthropod	33	42	33	43	22	23
Total no. items					64	304

in the 1990s than in the 1970s. Third, otters increased in number and still relied on aquatic prey while mink decreased in number and shifted toward terrestrial prey. These considerations support the hypothesis that the shift of mink toward a more terrestrial-based diet was mainly due to the presence of higher otter densities, and therefore to increased intra-guild competition, rather than to the lack of aquatic prey or to an increase of terrestrial prey.

Table 3. Niche breadth and niche overlap of otter and mink. All prey items were included in the calculations except for 'vegetation', which is probably ingested incidentally. In the last two rows niche breadth and niche overlap were recalculated excluding earthworms, arthropods and molluscs.

Year	Niche breadth		Niche overlap
	Mink	Otter	
1972–73 (all items)	0.15	0.05	0.93
1998–89 (all items)	0.25	0.14	0.81
1972–73 (small items excluded)	0.16	0.05	0.93
1998–89 (small items excluded)	0.25	0.10	0.74

We found that in winter mink considerably shifted their diet toward terrestrial prey items when at higher otter densities, but that their diet remained practically unchanged in spring, irrespective of otter densities. Bearing in mind that the sample sizes for this analysis were relatively small, this result suggests that competition was likely to have a stronger effect on the choice of prey items by mink in winter than in spring, with mink possibly avoiding the hunting grounds of otters at a time of the year when resources for these species are particularly restricted (Kruuk 1995). A lower niche overlap in winter than in spring was also found by Jedrzeijewska et al. (2001) studying otter and mink in Poland, while Erlinge (1972) studying otter and mink in Sweden found that niche overlap was greater in winter than in summer. In those cases where the stronger competitor can aggressively defend resources, we would expect a lower niche overlap during periods when resources are particularly limited because it is at this time of year that they would be more strongly defended. It is possible that on the river Teign and in the Polish study areas, otters could actively defend resources in winter, while for some reason this was not possible in Sweden.

Effect of other factors on the diet of mink

A similar pattern in the diet of mink, involving an increase in niche breadth and a decrease in niche overlap at higher otter densities, was observed by Clode and Macdonald (1995) in the Scottish Islands. The degree of niche overlap both at high and low otter densities was much lower in their study (0.71 for allopatric populations – 0.59 for sympatric populations) than in our study (0.93 for allopatric populations – 0.81 for sympatric populations). This can be due to several factors such as differences in prey composition between the two locations, seasonal differences, differences in the density of the two species, and in their hunting behaviour. Seasonal differences probably played a role. Clode and Macdonald (1995) conducted their study in the summer, when resources were more abundant and therefore competition was likely to be less intense. The data used in this study were instead mostly from the winter and spring seasons, when resources were scarcer (Kruuk 1995) and competition was likely to be more intense. The lower niche overlap in the Scottish Islands might also be partly due to the fact that in coastal habitats, where the study of Clode and Macdonald was conducted, mink tend to hunt in the intertidal area while otters hunt in the sea (Bonesi et al. 2000), thereby favouring the selection of different prey species and consequently a lower niche overlap. Instead, in a riparian habitat, such as the one of this study, both otter and mink feed in the same areas and therefore are likely to catch more of the same prey. Another possibility is that the level of otter density may also be important in determining the level to which the diet of mink shifts when in the presence of otters. Clode and Macdonald found a much larger shift in the diet of mink at higher otter densities compared to the present study. For example, in their study the difference in the frequency of occurrence of fish between allopatric and sympatric populations of mink was 60 (112–52), while in our study it was 20 (50–30). This difference may be explained by the fact that the densities of otters were higher on the Scottish Islands, where Clode and Macdonald conducted their study, than on the river Teign, which is an oligotrophic river thereby able to sustain only low otter densities (Kruuk et al. 1993). It is possible that higher densities of otters may have forced the mink to shift its diet to a greater extent to reduce the effects of competition, as predicted by the theory of habitat selection (Abramsky et al. 1991, Rosenzweig 1981). While the shift needed not to be so large on the river Teign where the density of otters, albeit greater than in the 1970s, was still relatively low.

Conclusions

We found that mink shifts its diet as otter density increases, thus suggesting that mink habitat use may be affected by competition with the otter. The results of this paper suggest that mink should be able to coexist for longer with the otter in areas where there are abundant alternative prey species that are not exploited by its competitor.

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