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Influence of spatial heterogeneity on coastal otter (*Lutra lutra*) prey consumption

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We studied otter diet in a heterogeneous coastal environment in S Spain including sandy and rocky coastal habitats as well as four small Mediterranean-regime streams. The main sources of environmental variation (rocky coast *vs*. sandy coast, coastal habitat *vs*. inland habitats) were clearly reflected in the otter diet composition. In rocky coastal transects otters intensely predated on wrasses, blennies and rocklings, while in sandy coastal ones eels, flatfish and crayfish were characteristic prey types. Grey mullet was the most important prey type in terms of biomass in both coastal environments. Fish consumption clearly decreased from coastal habitat to inland ones. Otter prey were heavier in coastal than in inland habitats, while consumed fish were heavier in the sandy coast than in the rocky one. Within the wide habitat variation in the study area, otter foraging efficiency was considered maximum in estuarine environments.

Introduction

Eurasian otters (*Lutra lutra*) inhabit a wide variety of aquatic environments, including freshwater as well as coastal ones (Mason & Macdonald 1986, Kruuk 1995). Coastal otters usually live at higher densities and occupy much smaller ranges than those inhabiting rivers and streams (Kruuk & Moorhouse 1991), apparently as a response to the increased availability of fish in coastal habitats (Kruuk & Hewson 1978). In their review on otter diet, Jędrzejewska *et al*. (2001) found a clear reduction of the importance of fish, the otter's staple prey, from coastal to inland habitats. However, Conroy and Jenkins (1986) and Beja (1991) proposed that foraging in brackish or freshwaters habitats could be energetically more rewarding for otters than foraging in the open sea. This would explain the average larger litter sizes of otters inhabiting freshwater habitats (Kruuk *et al*. 1987, Beja 1996a). Nevertheless, direct comparative studies on the use of inland and coastal food resources by otters are scarce, making it difficult to extract strong conclusions. Moreover, most studies on the diet of otters living in marine areas have been conducted in rocky coast environments, while reports of the same in sandy coastal areas are extremely scarce.

In this work, we studied the diet of an otter population inhabiting an heterogeneous coastal environment, which includes sand beaches, rocky

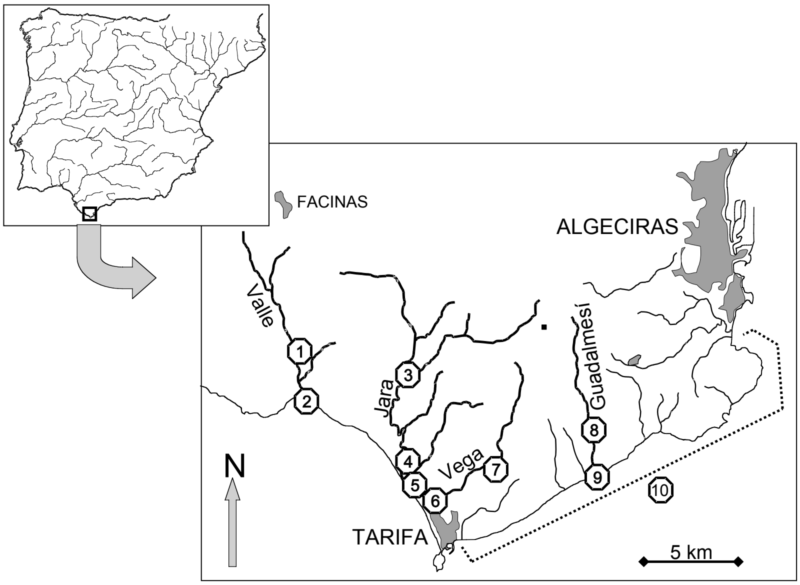

Fig. 1. Map of the study area showing the location of the ten transects where diet of otters was investigated.

coast and four main, but short, water courses. These suffer intense flow fluctuations, following the Mediterranean precipitation regime, being reduced to isolated pools in the summer. To date, no otter diet study has analysed the use of trophic resources by this mustelid in a small area including such a variety of habitats. The main objectives of this study are: (1) to thoroughly describe otter diet in the area, and (2) to analyse the spatial patterns in otter feeding habits in relation with the environmental differences between (i) rocky and sandy coastal areas and (ii) coastal areas and small Mediterranean-regime streams.

Study area

This study was carried out in the surroundings of Tarifa, the southernmost town in Europe (36°00´N, 5°36´E). The area comprises a coastal band about 30 km long and 5 km wide that runs from the El Valle river to the city of Algeciras and includes four small water courses: El Valle, La Jara, La Vega and Guadalmesí (Fig. 1). The average annual rainfall is highly variable within the study area (1396 mm, 1019 mm, 737 mm and 616 mm in the four stations included in the area) due to the abrupt relief, while mean annual temperature is rather constant among stations, being around 17.5 °C (Ibarra 1993). Vegetation is dominated by wild olive trees (*Olea europaea* var. *sylvestris*), cork oaks (*Quercus suber*) and different kinds of Mediterranean shrubland. The main land use is extensive cattle raising and there is a growing tourism industry.

Two different sectors can be defined in the area, mainly according to their topography and the coastal physiography: (i) from Tarifa to the northwest the coast is an almost continuous sandy beach, where rivers form relatively extensive estuaries with associated marshes. Rivers La Jara and La Vega share a common estuary, while El Valle flows into a coastal lagoon that only occasionally meets the sea; (ii) from Tarifa to the northeast the area is characterised by the steep relief (reaching 900 m above sea level) and the abrupt rocky coastal fringe. Many small streams flow into this section, but most of them are dry through most of the year.

Methods

We studied otter diet by analysing its faeces (spraints). We collected otter spraints in nine 600-m-long transects, located in the lower and middle sections of the four studied rivers (8 transects) and in the common estuary of rivers La Jara and La Vega (Los Lances). Additional samples were collected in the rocky coastal stretch between Tarifa and Algeciras (Fig. 1). This last transect was much longer than the other nine, but we found spraints almost exclusively in stream mouths, and not along its whole length. Four transects (numbers 2, 4, 5 and 6 in Fig. 1) corresponded to the coast in the western sandy sector, two (9 and 10) to the coast in the eastern rocky sector, and the remaining four to inland small streams of the western (1, 3 and 7) and the eastern (8) sectors. The terms *upper* and *lower* were used to differentiate the coastal (lower, both rocky and sandy) from stream (upper) transects (Table 1). Spraints were collected bimonthly from December 1999 to December 2002.

Spraint analysis followed standard procedures (Beja 1997). We identified prey remains using published keys (Webb 1980, Roselló 1986, Prenda *et al*. 1997) and our own collection for comparison. We considered each identified prey class in a spraint as an "occurrence", and expressed general diet as *frequency of occurrence* (FO, number of occurrences of a certain prey type divided by number of spraints analysed) or as *relative frequency of occurrence* (RFO, number of occurrences of a certain prey type divided by total number of occurrences of all prey types) (Mason & Macdonald 1986). Though RFO is the most direct method to compare diet composition in different areas (Jędrzejewska *et al*. 2001, Clavero *et al*. 2003), the lack of independence of the relative frequencies of the considered prey types (they sum 100) is a problem that affects the interpretation of the variation in the importance of the different prey types. This problem is avoided by using FO, and its values were therefore used in the statistical analysis involving frequencies of occurrence.

We estimated the minimum number of individuals of each prey type in a spraint from the number and position (left–right) of diagnostic hard parts (mainly mouth bones for fishes, uropods for crayfish and shrimps, maxillipeds for

Table 1. Main characteristics of the 10 transects selected in the study area for the analysis of otter diet. Number codes are as in Fig. 1.

Transect		Brief description
1	Upper Valle	Slow flowing stretch. Flow stops during the summer, when water only remains in a series of isolated pools. Presence of loaches, sandsmelts and eels. Crayfish very abundant. Densely vegetated, with dominance of willows and brambles.
2	Lower Valle	Coastal lagoon which is only occasionally in contact with the sea. Estuarine fish species present, though not abundant. Crayfish only occasionally present. Intensely used for camping, especially during the summer.
3	Upper Jara	Densely vegetated stretch, with willows and alders as dominant trees. It maintains some flow during summer in rainy years. Presence of chubs, loaches and eels. Crayfish abundant.
4	Lower Jara	La Jara river mouth, which is influenced by tide in all seasons. Margins dominated by Spartina. Estuarine fish species abundant. Crayfish absent. There is a camping area in the surroundings.
5	Los Lances	Common estuary of rivers La Jara and La Vega, which forms a coastal lagoon in Los Lances beach. Estuarine fish species abundant. Crayfish absent. Almost continuously in open contact with the sea.
6	Lower Vega	Transitional zone between the freshwater stream and the tide influenced area, though big tides might cover the whole transect. Estuarine fish species. Presence of loaches. Crayfish scarce.
7	Upper Vega	Seasonally flowing stretch, even pools become dry in the summer. Loaches, chubs and crayfish present though very scarce. Treeless margins, dominated by oleanders.
8	Upper Guadalmesí	High sloped stream, with a dense alder cover. Summer drought buffered by orogenic fogs. Presence of eels. Chubs extremely scarce, crayfish absent.
9	Lower Guadalmesí	Guadalmesí river mouth in a rocky coast. Strong changes in salinity due to reduced or null summer flow. Estuarine fish species. Freshwater fish and crayfish absent.
10	Rocky coast	Long and homogeneous rocky coastal transect with many small stream mouths with ephemeral flow. Freshwater fish and crayfish absent except in one stream.

marine crabs and illions for amphibians) (Beja 1996b). We measured these key structures to the nearest 0.1 mm. When diagnostic pieces did not appear, we considered that remains of a certain prey type belonged to a single individual.

We applied regression equations to estimate the original weight of the prey consumed by the otter. We computed regressions between the size of key structures (mouth bones and vertebrae for fish and uropod's endopodite for crayfish) and original length ($y = a + bx$) and between length and weight ($y = ax^b$) (Prenda & Granado 1992, Prenda *et al*. 2002; P. R. Beja and own unpubl. data). We estimated crayfish weights excluding claws, since they were rarely found in spraints (*see* also Watt 1991 and Beja 1996). We estimated the weights of ingested marine crabs by direct regression between the third maxilliped's meros size and crab weight (without claws) computed from a sample of shore crabs (*Carcinus maenas*) (own data). When some individual lacks measurable remains, we used the median weight of that prey type in the same transect for calculations. All the r^2 values of the equations used to estimate both original lengths and weights were above 0.90, and the minimum number of individuals included in the regression analyses was 16.

We assigned constant weights to the remaining prey types: small common gobies (*Pomatoschistus* sp.), insects, shrimps and other small arthropoda, 1 g; frogs (*Rana perezi*) 20 g; toads (*Bufo bufo*), 50 g; spadefoot toads (*Pelobates cultripes*) and urodela, 10 g; tree frogs (*Hyla meridionalis*) and Iberian parsley frogs (*Pelodytes ibericus*), 5 g; water snakes (*Natrix maura*), 50 g, terrapins (*Mauremys leprosa*), 100 g; birds, 100 g (following Beja 1996b).

We calculated the mean biomass per spraint (total biomass ingested divided by the number of spraints analysed) in each transect. We used this index as an indirect estimator of foraging efficiency, since high values indicate frequent captures of large prey, independently of the fact that small prey could be simultaneously consumed.

We performed a principal components analysis (PCA) to describe the main sources of variation in otter's diet composition and to study their possible relation with the environmental heterogeneity found in the study area. We ran two different PCAs, one using FO and another with percentage of biomass of the different prey types. Prior to PCA we arcsine transformed both FO and percentage of biomass values (Zar 1984). We assumed that the prey found in spraints from a certain transect were consumed in the same transect.

Whenever data did not meet assumptions for parametric statistics, we employed non-parametric tests.

Results

Food spectrum

Over the study period we analysed 1682 spraints, comprising 3332 occurrences of 40 different prey types and grouped them in 18 basic prey types (Table 2). We identified a minimum of 5742 individuals of the different prey types, summing a total biomass of 125 kg. The different methods used to estimate the otter diet composition showed rather high agreement, especially FO and percentage of individuals, which produced almost identical results ($r_s = 0.93$; $P < 0.001$). The similarity between other methods was still high as shown by rank correlation (percentage biomass-FO: $r_s = 0.84$, $P < 0.001$ and percentage individuals-percentage biomass, $r_s = 0.68$; $P < 0.01$).

Fish was the most important prey, constituting 58.7% of all the occurrences. Eels (*Anguilla anguilla*) (RFO = 12.6%), grey mullets (Mugillidae) (11.4%), flatfish (Soleidae) (7.7%) and wrasses (Labridae) (7.6%) were the most frequently consumed fishes, though gobies (Gobiidae) (6.2%) and blennies (Blenniidae) (5.2%) were also common. Freshwater fish (chub, *Squalius pyrenaicus*, and loach, *Cobitis paludica*) were a minor component in otter diet (2%). Nevertheless another freshwater prey, the red swamp crayfish (*Procambarus clarkii*), was the most frequently consumed of all the identified prey species, making up 22.5% of the occurrences. Amphibians were the next prey type in importance accounting for 6.5% of the occurrences, followed by small crustaceans (mostly shrimps, 5.1%), and marine crabs (4.2%). Insects (2.8%) and reptiles (1.8%) were less frequent, while only one spraint contained bird remains.

In terms of biomass, fish constituted the most

Table 2. Otter diet in the study area expressed as frequency of occurrence (FO), relative frequency of occurrence (RFO), proportions of individuals (IND) and biomass (BIO) of the main prey types, and relative frequency of occurrence (RFO) of the same in the different studied transects. Number of spraints analysed in each transect are also specified in the last row. Number codes are the same as in Fig. 1.

		FO	RFO	IND	BIO	1	2	3	4	5	6	7	8	9	10
Fish		59.8	58.7	50.3	78.9	15.7	26.1	33.6	58.3	80.2	71.8	24.1	55.3	90.0	94.7
Eel	*Anguilla anguilla*	25.0	12.8	11.5	17.0	8.2	13.4	12.7	20.9	19.4	21.1	15.2	10.6	1.1	3.0
Grey mullets	Mugilidae	22.6	11.5	8.5	36.0	2.9	7.2	7.2	13.2	22.8	17.2	3.4	2.1	13.2	11.8
Flatfish	Soleidae	15.2	7.7	6.5	11.1	–	0.7	5.1	10.6	25.1	22.8	1.4	–	–	0.3
Gobies	Gobiidae	12.3	6.2	7.8	2.1	0.3	2.6	1.1	5.6	6.5	5.2	1.4	4.3	10.7	17.6
Wrasses	Labridae	14.1	7.6	5.7	6.4	–	–	–	–	–	–	–	17.0	29.1	26.9
Blennies	Bleniidae	10.3	5.2	5.0	1.3	–	–	–	0.2	–	–	–	8.5	20.7	19.6
Rocklings	Gadidae	2.9	1.4	0.9	2.1	–	–	–	–	–	–	–	4.3	5.2	5.8
Sand smelt	*Atherina* sp.	1.0	0.5	0.5	0.1	–	0.3	0.4	1.5	0.8	0.9	–	–	–	–
Chub	*Squalius pyrenaicus*	2.1	1.1	1.0	0.9	–	–	4.0	2.2	0.8	1.3	2.8	–	–	–
Loach	*Cobitis paludica*	1.8	0.9	0.7	0.1	2.1	1.3	2.5	1	0.4	0.9	–	–	–	–
Other fish		7.0	3.7	2.2	1.9	1.1	0.3	1.8	2.0	2.7	1.5	–	8.5	10.0	10.1
Crustaceans		58.0	30.0	40.8	12.1	63.8	63.8	55.8	32.1	18.3	21.5	20.0	–	5.2	3.5
Red s. crayfish	*Procambarus clarkii*	44.6	22.8	21.7	10.5	51.1	44.0	55.4	25.7	11.8	13.3	18.6	–	–	1.0
Marine crab		4.9	2.1	1.3	0.8	–	1.3	–	2.6	1.9	4.5	–	–	3.9	1.5
Small crustaceans		10.0	5.1	17.8	0.8	12.8	18.6	0.4	3.8	4.6	3.7	1.4	–	1.4	1.1
Amphibians		13.0	6.5	5.7	4.8	12.0	4.2	8.3	7.8	2.3	4.5	26.2	23.4	2.3	1.0
Reptiles		3.6	1.8	1.0	4.0	1.9	3.3	0.4	1.3	0.8	1.7	14.5	2.1	0.5	–
Insects		5.5	2.8	2.0	0.1	7.2	2.9	0.7	1.5	0.4	1.1	13.8	19.1	2.0	0.5
Birds		0.0	0.0	0.0	0.1	–	–	–	0.2	–	–	–	–	–	–
						226	190	182	278	118	227	70	28	210	164

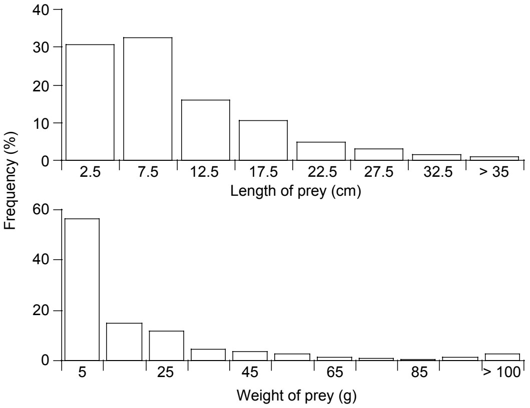

Fig. 2. Frequency distribution of estimated lengths (5-cm intervals) and weights (10-g intervals) of prey consumed by the otter in the study area ($n = 5742$).

important component of otter diet, representing almost 80% of the total biomass consumed. Grey mullets were the prey type that provided the most important bulk of ingested biomass, with more than 35% of the total. Other important biomass contributions among fish corresponded to eels (17%), flatfish (11.1%) and wrasses (6.4%), while the rest of fish categories reached 2% or less. Crayfish was the other important prey type in terms of biomass consumed by the otter (10.5%), though its importance in biomass contribution is reduced when compared with frequency of occurrence data.

Prey consumed by otters were usually small, with a median length of 7.4 cm (mean = 10.2 cm) (Fig. 2). More than 70% of consumed prey were smaller than 10 cm long, with only 2.3% being longer than 30 cm. Median weight of consumed prey was 8.7 g (mean 21.0 g). Almost 60% of prey weighed less than 10 g. Though less than 3% of predated individuals ($n = 144$) were heavier than 100 g, this group accounted for 28.6% of the total biomass ingested by otters. Among this group, 78.5% were grey mullets, 14.6% eels, 5.6% flatfishes and 1.2% chubs (Fig. 3).

Spatial patterns in diet composition and prey size

We included in the PCAs the prey types shown in Table 1, with the exception of *other fish* and *birds* ($n = 16$). The two PCAs performed, using either FO or biomass proportion data, produced almost identical results. The first two components of both analyses showed very strong correlations (r above 0.96, $P < 0.001$) and were influenced by the same prey types. Thus, we considered that main diet patterns were the same using FO and biomass data, and the following analyses employed the FO matrix.

There were strong differences in otter diet composition among the studied transects (Table 2). The PCA, which produced two axes (PC1, PC2) that explained almost 75% of the original variance among transects, clearly reflected these differences (Fig. 4). The two main sources of environmental variation found in the study area were represented in PCA's results. PC1 (43% explained variance) was related to the coastal structure, clearly discriminating between transects corresponding to the western and the eastern sectors in the study area. Otters consumed wrasses, blennies and rocklings (Gadidae) exclusively in the eastern (rocky) sector, where eels, flatfish, freshwater fish (both chub and loach) and crayfish were rare or completely absent. Grey mullets were the only prey type that made an important bulk of the otter diet in both sectors of the study area. On the other hand, PC2 (30% explained variance) separated, both in the rocky and sandy sectors, transects placed in inland stream stretches, with a high frequency of insects and amphibians, from those placed near the coast, where grey mullets and marine crabs were characteristic prey. Both PC1 and PC2 were significantly correlated with the FO of fish ($r = -0.66$ and $P < 0.05$; and $r = 0.64$ and $P < 0.05$, respectively).

Otter prey were heavier in the rocky sector of the study area (median weight 17.0 g) than in the western sandy one (8.7 g) (Kruskal-Wallis ANOVA: $\chi^2 = 257.8$, d.f. = 1, $P < 0.001$). However, fish with estimated original weights were significantly heavier in the sandy sector than in the rocky one (medians 24.7 g and 14.4 g; K-W: $\chi^2 = 48.5$, d.f. = 1, $P < 0.001$). Though overall median prey weight was the same in the upper and lower stretches (8.7 g), there were significant differences between the two groups of transects (K-W: $\chi^2 = 94.7$, d.f. = 1, $P < 0.001$), due to a higher proportion of big prey in lower stretches.

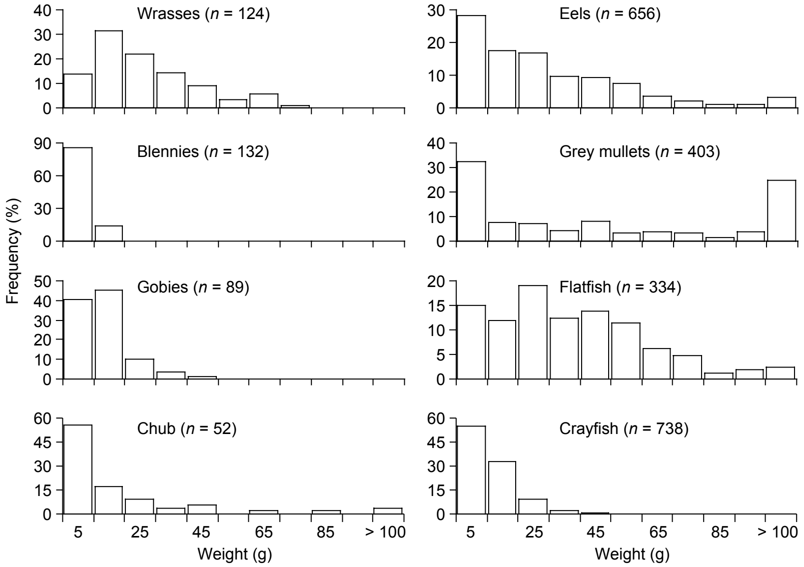

Fig. 3. Frequency distribution of estimated weights (10-g intervals) of crayfish and the main fish types consumed by the otter in the study area.

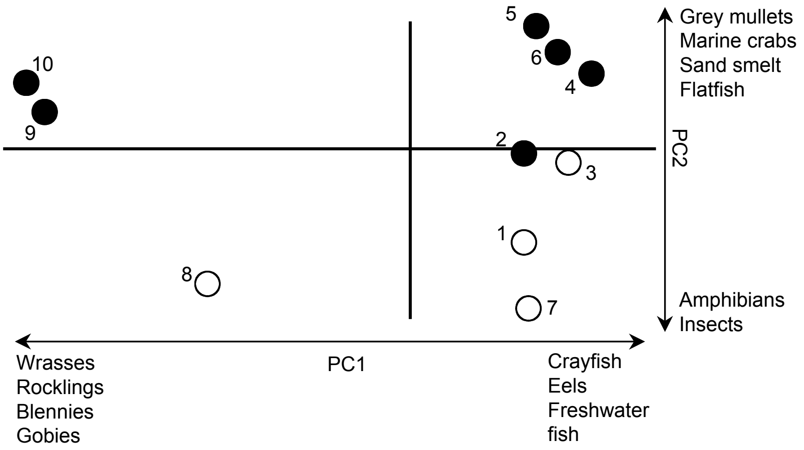

Fig. 4. Plot of the ten studied transects in relation with the first two principal components extracted from FO data of 16 prey types. Prey types whose FO are significantly correlated with PCs are shown. Numbers coding the different transects as in Fig. 1, and transects situated in upper stretches (white dots) are differentiated from those placed in lower ones (black dots). PC1: eigenvalue = 6.91; 43.2% expl. variance. PC2: eigenvalue = 4.92; 30.7% expl. variance.

The mean biomass per spraint showed clear differences among transects. Observed values were significantly higher in the lower stretches than in upper ones ($t = 3.0$, $P < 0.05$). Among the identified prey types, mean biomass per spraint was correlated only with the FO of grey mullets ($r = 0.85$, $P < 0.01$) and flatfish ($r = 0.77$, $P < 0.01$) (Fig. 5). The overall fish FO did not show any significant relation with this index.

Discussion

Limitations of the data and assumptions

Recent works (Carss & Parkinson 1996, Jacobsen & Hansen 1996) tested the accuracy of different methods of analysis of otter diet, concluding that results using frequency of occurrence methods (either FO or RFO) could imply deviations from the original diet composition. However, Jacob-

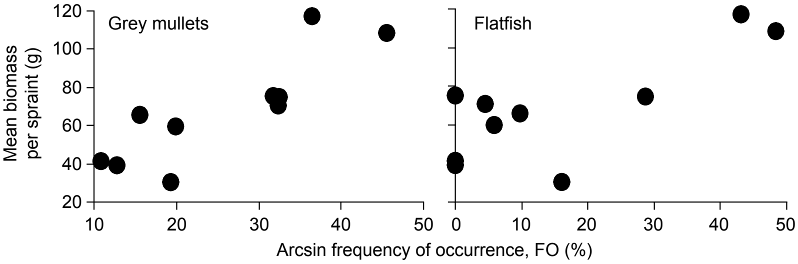

Fig. 5. Relation between foraging profitability, estimated from the mean biomass per spraint, and the frequency of occurrence of grey mullets and flatfish in otter diet in the ten studied transects.

sen and Hansen (1996) found strong similarities (above 85%, Renkonens Index of Similarity) between RFO and the other four methods tested, and argued that results obtained by the use of the different methods could be compared "in broad outlines". Nevertheless, Carss and Parkinson (1996) criticised the use of frequency of occurrence data for their lack of accuracy, and proposed as an alternative the use of key bones of the main prey. We used these key structures for determining the minimum number of individuals of most prey types consumed by the otter. We usually looked for a pool of key pieces for each prey type (i.e. 3 for crayfish, 4 for grey mullets and up to 8 for eels). The results using the frequencies of occurrence and percentage of individuals were however almost identical. We also eliminated another source of bias not considering the appearance of fish scales in a spraint as an occurrence, since Carss and Parkinson (1996) found that scales of a single fish were present in otter spraints for up to 10 days. The strength and spatial coherence of the ordination produced by the PCA presented here showed that solid patterns in diet composition can be described using frequency of occurrence data. Moreover, the almost identical patterns produced by the two PCAs performed (using FO and biomass proportion data) strongly reinforce this assumption.

Carss and Elston (1996), Jacobsen and Hansen (1996) and Carss and Nelson (1998) also analysed the accuracy of the estimations of original sizes of fish consumed by the otter. Jacobsen and Hansen (1996) concluded that the method proposed by Wise (1980) gave an appropriate image of the original size distribution of fish consumed, and could therefore be used in otter spraint analysis. However, Carss and Elston (1996), working with salmonids and eels, found the method inaccurate, based on the size-related probability of bone recovery. These two works used Wise (1980) estimations of fish lengths from vertebrae measurements. The method could be certainly improved by the combined use of a pool of structures to estimate original lengths, mainly fish mouth bones (premaxillae, maxillae, dentary) (Prenda & Granado 1992, Prenda *et al.* 2001), as done in this study (*see* also Beja 1997). Similar methods were recently used also to estimate the original size of crayfish consumed by the otter and other predators (Beja 1996b, Correia 2001).

The critical assumption that each prey identified in a certain transect was consumed there might be theoretically inaccurate, since otters could easily cover the distance between many transects daily (Kruuk 1995, Ruiz-Olmo *et al.* 1995). In fact we identified some prey types that were obviously consumed far from the transects where the spraint that contained their remains was collected. However, this assumption is conservative, since the mixture of spraints among transects would tend to soften the possible spatial patterns in otter diet in the study area.

Diet composition

The results presented here show the adaptability of the otter to feed on very different food resources in a reduced space. In a few kilometres, otter diet shifted from an almost exclusive piscivory to a strong predation on crayfish or amphibians. However, the overall frequency of fish was very low when compared with most otter diet studies, especially those from coastal areas (i.e. Heggberget & Moseid 1994, Watt 1995, Beja 1997, Kingston *et al.* 1999). This was mainly caused by the high frequency of red swamp crayfish, an alien and invasive species in Iberian freshwater systems that has experienced a rapid spread since its introduction in Spain in the mid 1970s (Hasburgo-Lorena 1983, Correia 1993). Crayfish is nowadays an important prey for the otter (Adrián & Delibes 1987, Delibes & Adrián 1987, Beja 1996b) and other mammalian and avian predators in the Iberian Peninsula (Correia 2001). In fact, it was the most frequent prey species in otter diet in the study area.

Other prey types that are marginal or absent in many otter diet studies were also frequently consumed in the area, such as reptiles or small arthropoda (both small crustaceans and insects). Predation on this last group was especially intense, summing an RFO of 8% and making up 20% of the individuals consumed by the otter. Up to 50 shrimps were sometimes identified in a single spraint. These observations agree with those made by Carss and Parkinson (1996), who confirmed that captive otters actively predated upon small aquatic invertebrates. Other small prey were also frequently consumed by the otter, as common gobies (3–5 cm length) that made up 5% of the consumed individuals. Delibes *et al.* (2000) also showed that very small prey, such as eastern mosquitofish (*Gambusia holbrooki*), were important prey for the otter in Doñana (S Spain).

Proportions of the main fish groups consumed by the otter were also different from most previously published studies. Flatfish are usually a minor prey type in most studies from coastal areas (Gormally & Fairley 1982, Kruuk & Moorhouse 1990, Beja 1991, Kingston *et al.* 1999), but they provided an important amount (over 10%) of the biomass ingested by the otter in our area. Also, grey mullets have been rarely cited as an important prey for the otter (Libois 1995), though Beja (1991) suggested that they could be considered the main prey of otters inhabiting Iberian brackish water habitats. In fact, grey mullet was the main otter prey in the study area, since it accounted for the most important proportion of the ingested biomass and was the only prey type frequently consumed in both sectors of the study area. In fact, grey mullets made the most important contribution in terms of biomass in the 6 transects placed near the coast. Moreover, most of the large fish (> 100 g) consumed were grey mullets.

Prey consumed in the sandy sector of the study area are responsible for most of the differences between this and other diet studies, since proportions of the different prey types in the rocky sector were very similar to those recorded in nearby rocky coastal environments in Portugal (Beja 1991, Beja 1997). The proportion of fish in this later sector was as high as that recorded in rocky coastal areas of many other European locations (*see* review in Jędrzejewska *et al.* 2001). The close relationship between otter diet and landscape characteristics underlines the importance of the spatial patterns in prey consumption detected in the study area.

Spatial patterns

Almost 75% of the variance observed in otter diet could be related with the two main sources of environmental heterogeneity of the area. The first PC discriminated transects placed in the rocky and sandy sectors of the study area. Otter diet in the former featured high proportions of rocky littoral fish (i.e. wrasses or blennies) that were not consumed in western transects, where crayfish, eels, flatfish and freshwater fish were characteristic prey. Freshwater fish and crayfish were almost completely absent in the eastern sector. The low otter predation on eels in the rocky coastal transects was surprising, since the species was present in many stream mouths and is abundant at least in the lower Guadalmesí river (Clavero *et al.* 2002). This observation seems contrary to previous suggestions that eel is a favourite otter prey whenever readily available (Adrián & Delibes 1987, Libois *et al.* 1991, Kruuk 1995).

Overall prey weight was higher in the rocky sector, due to the low occurrence of many small sized prey that were frequent in the western sector (i.e. shrimps and common gobies) and the almost null predation on crayfish, which was lighter than most fish consumed by the otter. The weight of predated fish was however higher in the sandy sector. This observation agrees with those made by Conroy and Jenkins (1986) who compared the fishing efficiency of otters in the open sea and in a freshwater loch and found that though otters captured individual fish faster in the sea, they performed shorter hunting sessions in freshwater. These authors suggested that the smaller size and lower caloric values of fish captured in the sea would account for the observed differences in hunting sessions' lengths. Then, though fish are apparently more easily caught in the sea (Beja 1991), foraging in freshwater and estuarine areas, as those present in the western sector, would be more profitable for the otter due to the capture of larger fish.

The other main source of environmental heterogeneity in the area is the sharply different conditions found between coastal transects (both estuarine and those in the rocky coast) and those placed in inland stream stretches, which follow a typical Mediterranean flow regime (Blondel & Aronson 1999). This gradient was clearly reflected in PC2, which separates transects placed in upper and lower stretches. In the later otter diet there featured higher proportions of grey mullets, marine crabs and, to a lesser extent, flatfish and sandsmelts (*Atherina* sp.). Diet in the upper stretches incorporated more amphibians and insects in parallel to a significant decrease in fish consumption. Jędrzejewska *et al.* (2001), in a review of several diet studies in the Palearctic range, reported a clear increase in fish consumption of coastal otter populations in relation with those in inland habitats. This pattern seems therefore to be constant and detectable at very different scales (M. Clavero *et al.* unpubl. data). The trend of decreasing fish consumption in inland habitats was certainly accentuated in the study area due to the environmental fluctuations, which are extreme in Mediterranean small streams (Gasith & Resh 1999, Magalhães *et al.* 2002). A relationship between frequency of fish in otter diet and the stability of aquatic ecosystems was also described in a large scale approach by Clavero *et al.* (2003), with a low fish consumption in the highly unstable Mediterranean freshwater habitats. The smaller weight of otter prey and the lower mean biomass per spraint, together with the reduced fish consumption, in the upper transects apparently suggest that foraging in streams is less profitable for otters than doing so in coastal habitats.

In conclusion, foraging was apparently more profitable for otters in lower than in upper stretches and in sandy coastal areas than in rocky coastal ones. Among the high environmental diversity present in the area, estuarine-brackish habitats would be the most efficiently exploited by otters. Spatial patterns in otter diet composition occurred in parallel to landscape characteristics, strongly reflecting the area's environmental complexity in spite of its reduced size.

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