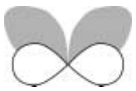
Journal of Biogeography, **30**, 761–769



Trophic diversity of the otter (*Lutra lutra* L.) in temperate and Mediterranean freshwater habitats

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Abstract

Aim To analyse the geographical patterns in the composition and diversity of otter's (*Lutra lutra* L.) diet and their relationship with climatic characteristics.

Location European freshwater habitats under Mediterranean and temperate climatic regimes.

Methods Thirty-seven otter diet studies were reviewed, twenty-one from temperate and sixteen from Mediterranean areas. All studies were based on spraint analysis and their results expressed as relative frequency of occurrence of seven main prey categories. Principal Component Analysis was performed to extract the main gradients of diet composition. Pearson's correlation and *t*-tests were used to assess the relationship between diet characteristics (composition, diversity and taxonomic richness) and geographical and climatic variables.

Results A clear latitudinal gradient in diet composition was observed. Otter diet was more diverse and featured more prey classes in southern localities, while the species was more piscivorous towards the north, where it predated upon a higher number of fish families. This pattern was similar when temperate and Mediterranean localities of Europe were compared. Mediterranean otters behaved as more generalist predators than temperate ones, relying less on fish, and more on aquatic invertebrates and reptiles.

Main conclusions Geographical differences in otter feeding ecology in Europe seem to be related with the two contrasted climatic conditions affecting prey populations. The otter can act as a highly specialized piscivorous predator in temperate freshwater ecosystems, which do not suffer a dry season and have a comparatively stable water regime compared to Mediterranean ones. However, the unpredictable prey availability in Mediterranean areas, affected by strong spatial and temporal water shortages, favours a diversification of the otter's diet.

Keywords
Feeding habits, freshwater ecosystems, freshwater fishes, geographical variation, otter, *Lutra lutra*, Mediterranean climate.

INTRODUCTION

The latitudinal gradient in diversity (i.e. an increasing richness of flora and fauna species from the poles to the tropics) is considered the oldest (Hawkins, 2001) and the best known (Rosenzweig, 1995) biogeographical 'pattern' in ecology. As abundance and diversity of potential prey are the most important features determining a predator's niche width (MacArthur & Pianka, 1966; Schoener, 1971), we could expect, on a large scale, that predator species occupying a broad geographical range may experience variations of their food-niche breadth following changes in prey communities. At the intraspecific level, such differential use of trophic resources among allopatric populations may occur with minor or no apparent morphological or physiological changes (Futuyma & Moreno, 1988; Martín *et al.*, 1995).

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Studies on the trophic ecology of several species of birds and mammals support the prediction of a decreasing trophic diversity at higher latitudes. A classical example is the puma (*Puma concolor* L.), whose range extends from Alaska in the north to Tierra del Fuego in the south and whose highest food-niche breadths are reached in tropical America (Iriarte *et al.*, 1990). In Europe, an increasing dietary diversity towards the south has been suggested for the barn owl (*Tyto alba* Scop.; Herrera, 1974), Montagu's harrier (*Circus pigargus* L.; Arroyo, 1997) and other raptors (Korpimaki & Marti, 1995), among the birds, and common genet (*Genetta genetta* L.; Virgós *et al.*, 1999) among the mammals.

As abiotic environmental factors, such as climate regime, are one of the most important determinants of the composition and structure of prey communities (Smith & Smith, 2000), the observed dietary patterns in Europe could be associated with the two principal climatic areas defined in the continent: temperate in central and part of northern Europe and Mediterranean in the south (Fig. 1). Temperate climate is characterized by cold winters and mild and rainy summers, without a summer drought. Mediterranean areas (the term 'Mediterranean' is always used in the text in a climatic, and not strictly geographical, sense), considered transitional between cold temperate and dry tropical zones, are characterized by the unique combination of hot dry summers and cool humid winters. Little or no surface water is available during the summer, generating a period of effective physiological drought. Added to this seasonality is a characteristic unpredictability, with dramatic variations of weather conditions between years, between seasons of a given year and even in the course of a single day (Blondel & Aronson, 1999).

Freshwater ecosystems are especially sensitive to predictable and unpredictable environmental variations such as those characteristic of Mediterranean climates (Prenda & Gallardo, 1996; Gasith & Resh, 1999; Magalhães *et al.*, 2002). Consequently, the Eurasian otter (*Lutra lutra* L.), a top predator of aquatic ecosystems, could experiment changes in its food and foraging behaviour according to the composition and structure of prey communities in Mediterranean and temperate ecosystems. The strong decline suffered by the populations of the otter in Europe since the 1950s has largely stimulated research into the species' distribution and ecology (Mason & Macdonald, 1986), diet being one of the central issues (Carss, 1995). Such a situation provides a good chance to analyse the possible variations in the otter's trophic diversity throughout Europe.

Mason & Macdonald (1986) suggested that otters in southern Europe featured more amphibians and reptiles in their diets than those of the north. Also, Adrián & Delibes (1987) indicated that frequency of occurrence of insects, amphibians and reptiles in faeces of otters in Europe seemed to increase as latitude decreased. Again, Ruiz-Olmo (1995) showed that reptiles were a common food of Mediterranean otters, but were very rare in other latitudes. However, a recent analysis of the diet of otters in Eurasia failed to detect

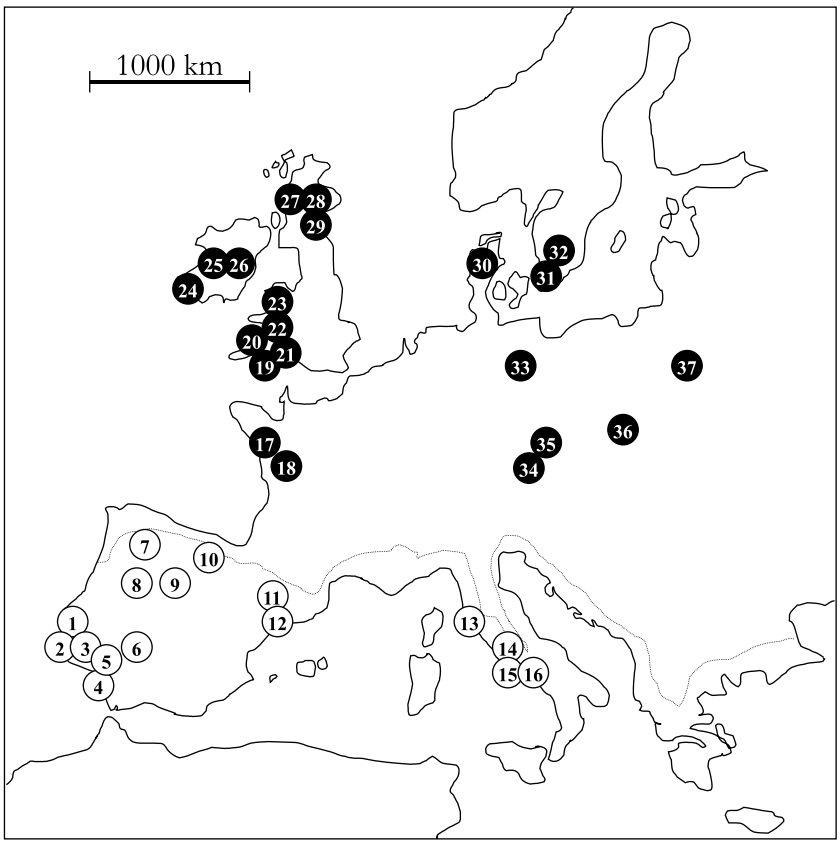

Figure 1 Distribution of the thirty-seven reviewed studies on the diet of otters (*Lutra lutra* L.). The dotted line separates temperate (filled circles) from Mediterranean locations (empty circles). The numbers are assigned to original works as follows. 1: Canas (1999); 2: Beja (1996); 3: Adrián & Moreno (1986); 4, 5: Adrián & Delibes (1987); 6: López-Nieves & Hernando (1984); 7: Morales & Lizana (1997); 8: Acera (1998); 9: Morales *et al.* (1998); 10: Callejo & Delibes (1987); 11, 12: Ruiz-Olmo *et al.* (1989); 13: Arcá & Prigioni (1987); 14–16: Prigioni *et al.* (1991); 17: Lodé (1989); 18: Libois (1995); 19, 20: Chanin (1981); 21: Wise *et al.* (1981); 22: Webb (1975); 23: Henshilwood (1981); 24: Gormally & Fairley (1982); 25: Kyne *et al.* (1989); 26: O'Neill *et al.* (1998); 27, 29: Weber (1990); 28: Carss *et al.* (1990); 30: Taastrøm & Jacobsen (1999); 31: Erlinge (1967); 32: Erlinge (1969); 33: Geidezis (1998); 34: Lanszki & Körmendi (1996); 35: Knollseisen & Kranz (1998); 36: Wisniowska (1996); 37: Brzeziński *et al.* (1993).

any of these trends (Jędrzejewska *et al.*, 2001). These authors stated that otter diets in Eurasia do not change with latitude, but change with habitat: fish are more frequent as prey on sea shores, followed by lakes, and rivers and streams; amphibians and crustaceans show just the contrary trend.

The aim of this paper is to search for geographical patterns in diet composition and diversity of otters living in Mediterranean and temperate climatic conditions in Europe. To remove the important bias that coastal otters can introduce, we limited our sources to freshwater habitats.

MATERIAL AND METHODS

Data on otter diet were taken from thirty-seven diet studies from the available literature (see Appendix). Each study area was assigned to Mediterranean or temperate climate conditions according to the map of Emberger *et al.* (1963). This resulted in sixteen Mediterranean and twenty-one temperate localities (Fig. 1). All the studies were based on spraint analysis and the data expressed as relative frequency of occurrence (RFO) (number of occurrences of a certain item as a percentage of the total number of occurrences of all prey items). Only studies with more than 200 occurrences of the different prey categories were considered. Usually, results from several places or streams from the same area were pooled to avoid pseudoreplication (Hulbert, 1984). Whenever necessary, original data were transformed to RFO to allow a correct comparison. Recent critical analyses (Carss & Parkinson, 1996; Jacobsen & Hansen, 1996) have shown that RFO is not the best method to assess otter diet, leading to overestimation of medium size prey items and underestimation of the smaller and bigger ones. However, Jacobsen & Hansen (1996) compared several methods and found that similarity of RFO results with those of more accurate methods was between 80% and 90% (Renkonens Index of Similarity). Thus, being the most frequent method used in literature, and for our aim of making comparisons, we consider RFO an appropriate methodology to establish dietary geographical patterns.

Seven basic prey categories were considered: fish, amphibians, reptiles, birds, mammals, crayfish and other aquatic invertebrates (beetles, damselfly nymphs, small shrimps, etc). For each local diet, we calculated the number of prey categories (NPC) and, when possible (in thirty-five studies), the total number of fish families (NFF) present in the sample. To quantify the general trophic diversity for each location, the Shannon–Wiener index (H′) applied to frequencies of occurrence was used.

Principal Component Analysis was performed to an arcsine transformed matrix of RFO × study locations ($n = 37$) in order to summarize general patterns in otter diet throughout the study area. RFO were arcsine transformed before the analysis to homogenize variances (Zar, 1984). Pearson's correlations between occurrence data, trophic and geographical variables and principal components were calculated. To assess differences between Mediterranean and temperate diets we used *t*-tests. Whenever multiple *t*-test were performed, significance levels were corrected using the Sequential Bonferroni test (Rice, 1989).

RESULTS

Fish were the otter's main food category, representing almost 75% of the consumed preys among otters inhabiting freshwater habitats (Table 1). The remaining categories can be considered as secondary in a general approximation to otter diet. Predation upon amphibians, crayfish and other invertebrates was frequent, while birds, reptiles and mammals were rather rare in the diet of the otter.

The first principal component (PC 1) produced a strong ordination of the different study locations, explaining 40% of the total observed variance. PC 1 defined a gradient running from high and almost exclusive fish consumption to relative high predation upon aquatic invertebrates, amphibians, crayfish and reptiles (Table 1). The diet gradient represented by PC 1 showed a marked geographical component, being highly correlated with latitude ($r = 0.63$; $P < 0.001$) (Fig. 2a). The second principal component explained only 17.6% of the observed variance and cannot be interpreted in geographical/ecological terms.

Latitude was also correlated with most prey items and trophic variables (Table 2). Fish consumption showed a strong positive correlation with latitude, a pattern shared with avian prey, while reptiles, crayfish and other aquatic invertebrates were consumed more at lower latitudes. The southward intensification of predation upon these four prey categories occurred in parallel to an increase in trophic diversity (Fig. 2b) and in the NPC in otter diet, and a decrease in the NFF (Table 2). Predation upon mammals and amphibians did not show any geographical pattern. Trophic diversity was negatively correlated with fish consumption and positively with the RFOs of amphibians, reptiles, crayfish and other aquatic invertebrates ($P < 0.001$ in all cases). The RFOs of mammals and birds were not related to trophic diversity.

Patterns in otter diet obtained by two-sample comparisons between Mediterranean and temperate climatic areas were similar to those shown by correlations with latitude

Table 1 mean relative frequency of occurrence for several otter (*Lutra lutra* L.) prey items in Europe and Pearson's correlation (*r*) between them and the principal component 1

Prey items	Mean ± SD	*r* Factor 1
Fish	72.8 ± 18.5	0.91***
Amphibians	8.8 ± 7.6	−0.68***
Reptiles	1.5 ± 2.9	−0.61***
Birds	1.9 ± 2.1	0.31 (NS)
Mammals	0.9 ± 1.3	0.43**
Crayfish	6.8 ± 12.9	−0.49**
Aquatic invertebrates	7.0 ± 7.7	−0.79***
Eigenvalue		2.80
Explained variance (%)		40.0

Significance levels: ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; NS, non-significant.

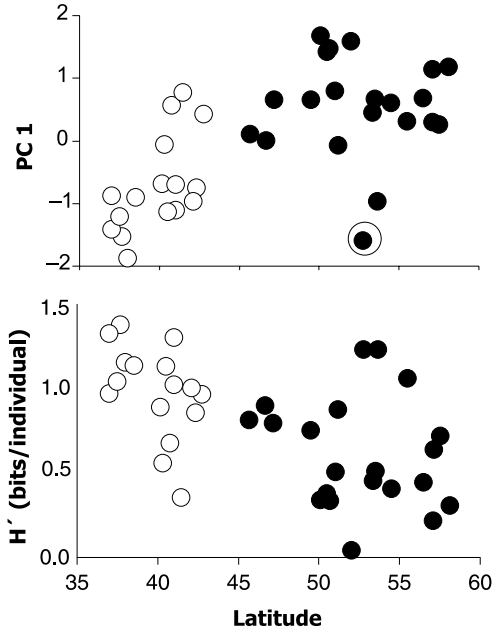

Figure 2 Relationship between latitude and (a) principal component 1 (PC 1) scores ($r = 0.63$; $P < 0.001$) and (b) trophic diversity, measured with the Shannon–Wiener index (H′), ($r = -0.57$; $P < 0.001$) for thirty-seven otter (*Lutra lutra*) diet studies. Filled circles: temperate locations; empty circles: Mediterranean locations. Encircled point (Brzeziński *et al.*, 1993; point 37 of Fig. 1) is commented in Discussion.

(Table 2). Mediterranean otters had more diverse diets and fed on a larger NPC and a smaller NNF than those occupying temperate habitats. The frequency of occurrence of fish and birds in otter diet was significantly higher in temperate than in Mediterranean locations, while the reverse happens with reptiles and aquatic invertebrates. Differences between Mediterranean and temperate locations in the consumption of crayfish, amphibians and mammals were smaller.

DISCUSSION

Although fish are the otter's main prey everywhere in Europe (Mason & Macdonald, 1986; Carss, 1995; Kruuk, 1995), their consumption shows on average a marked decrease in southern localities. This is compensated for by more intense predation upon a pool of alternative prey, including crayfish, reptiles, amphibians and aquatic invertebrates. Some of these alternative prey can constitute the bulk of otter diet in some southern places. As a consequence, Mediterranean otters show higher trophic diversity, predating upon a larger NPC than those of temperate habitats.

According to the latitudinal gradient in diversity, an increased trophic diversity of the otter in southern latitudes could also be related to a higher abundance and availability of non-fish prey in these areas. In fact, at least reptiles and insects are especially abundant in Mediterranean Europe (Blondel & Aronson, 1999), where the warm weather conditions allow them to reach large sizes and to be active most of the year. Moreover, the recent spread of the introduced American crayfish (*Procambarus clarkii*, Girard) has changed the diet of otters and other predators in many Mediterranean habitats (Delibes & Adrián, 1987; Beja, 1996; Correia, 2001), crayfish becoming an important prey.

However, a higher availability of alternative prey makes possible, although does not imply, an increase of trophic diversity. In addition, this usually necessitates a reduction in the abundance or availability of the preferred prey (Stephens & Krebs, 1986). Erlinge (1968) stated that captive otters preferred to predate upon fish, and apparently fish are the otter's staple prey whenever abundant, even under Mediterranean conditions. In fact, otters have an almost exclusive piscivorous diet in some Mediterranean localities where alternative prey are probably abundant (see Ruiz-Olmo *et al.*, 1989; Prigioni *et al.*, 1991). In the same way, otters in temperate areas feed on a high diversity of prey when availability of fish is reduced, like in Bialowieza, Poland (Brzeziński *et al.*, 1993; see Fig. 2). Kruuk (1995) also related a increase of non-fish prey with periods of low fish abundance in Scottish rivers.

		t-test results (mean ± SD)		
	Latitude (*r*)	Temperate ($n = 21$)	Mediterranean ($n = 16$)	*t*
Fish	0.51***	80.6 ± 15.5	62.6 ± 17.5	3.36*
Amphibians	−0.16 (NS)	8.2 ± 9.0	9.6 ± 5.3	1.01
Reptiles	−0.71***	0.1 ± 0.2	3.3 ± 3.7	6.82*
Birds	0.36*	2.6 ± 2.3	1.0 ± 1.2	2.77*
Mammals	0.16 (*NS*)	1.1 ± 1.3	0.7 ± 1.3	1.61
Crayfish	−0.38*	2.9 ± 6.8	11.8 ± 17.0	2.41
Aquatic invertebrates	−0.51***	4.3 ± 5.9	10.5 ± 8.7	2.64*
H′	−0.57***	0.62 ± 0.35	0.98 ± 0.28	3.62*
NPC	−0.55***	5.1 ± 1.15	6.2 ± 0.58	3.51*
NFF	0.56***	5.3 ± 1.38	3.7 ± 0.79	4.18*

Table 2 Pearson's (*r*) significant correlations between latitude and RFOs of general prey items in otter diet, trophic diversity (H′), number of prey items in otter diet (NPC) and number of fish families in otter diet (NFF). Significance levels for *r* values as for Table 1. Comparisons of the different variables under different climatic conditions using *t*-test are also shown. Significance levels for marked (*) *t* values, after Sequential Bonferroni test (ten tests)

We argue that the low or unpredictable availability of fish in freshwater Mediterranean ecosystems, more than the high abundance of alternative prey, favours the increased trophic diversity of Mediterranean otters. The harsh environmental conditions during the pronounced summer drought are a key factor explaining the composition and dynamics of Mediterranean freshwater communities (Prenda & Gallardo, 1996). Most streams and small rivers become dry or break into isolated pools during the summer, reducing the availability of fish (Pires *et al.*, 1999). Besides, the high intra- and interannual variability in the precipitation and temperature regimes characteristic of Mediterranean areas severely affects freshwater ecosystems, necessarily resulting in unpredictable fish availability (Mooney, 1981; Prenda *et al.*, 2001). In fact, otter diet in some Mediterranean areas have been shown to reach its maximum diversity during the summer, when fish populations are strongly affected by drought (Ruiz-Olmo *et al.*, 2001). Thus, the widening of the otter's feeding niche in Mediterranean ecosystems would be favoured in an environment where fish populations are temporally scarce and patchily available, both in space and time (see Erlinge, 1986). Sulkava (1996) described a very diverse diet of otters in central Finland ($H' = 1.16$) (see Table 2), in a taiga environment where the extremely cold winters produce great variations and unpredictability of fish availability (this work was not included in the analyses because central Finland cannot be considered a temperate area).

The review on otter diet by Jędrzejewska *et al.* (2001) did not find any relationship between diversity or composition of otter diet and latitude, but concluded that otters behave as more generalist predators in streams and rivers than in lakes and sea shores, where fish are more frequent prey. This conclusion supports our hypothesis in an indirect way, as it relates changes in the otter's trophic diversity with habitat features, especially the stability of water availability and its effects on fish abundance. We hypothesize that intra- and interannual abundance and predictability of fish resources could range from a maximum in sea shores and lakes to a minimum in Mediterranean temporal streams, being intermediate in temperate water courses; this should be accompanied by changes in the pattern of use of fish, its favourite prey, by the otter (Fig. 3).

Several reasons (the criteria to select the dietary studies, the covered range, the oversight of including reptiles, etc.) help to explain why Jędrzejewska *et al.* (2001) failed to describe the evident temperate–Mediterranean change in otter trophic niche breadth. However, the main cause probably was the low proportion of Mediterranean localities included in their analysis: only nineteen of 102 diet studies came from Mediterranean areas, and only twelve of them correspond to freshwater ecosystems. As the observed latitudinal pattern seems not to be gradual, but related to the different conditions in Mediterranean and temperate ecosystems, the pattern may be concealed if the proportion of localities is very biased towards temperate places (see Fig. 2 to note that in our study a latitudinal trend can be detected within Mediterranean localities, but is not apparent when only temperate ones are considered). Thus, Jędrzejewska

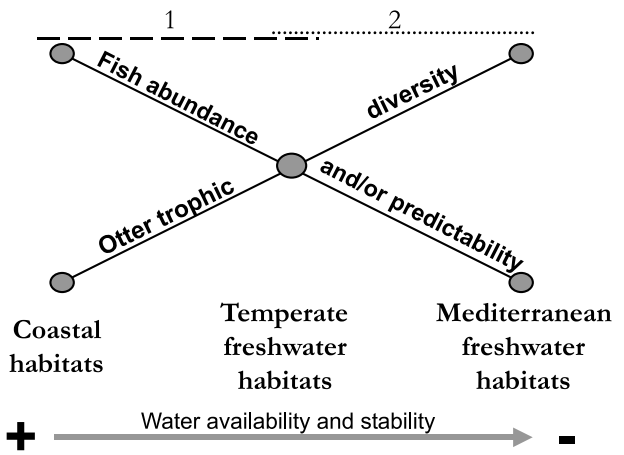

Figure 3 Schematic diagram representing the suggested variation in otter trophic diversity and fish communities characteristics in Europe in relation to water availability and stability. An amplification in otter trophic diversity is observed as fish become scarce or unpredictably available. Numbers show the habitats in which the review by Jędrzejewska *et al.* (2001) (1) and this study (2) were centred.

et al. (2001) could detect the increase in otter trophic diversity from sea-shores and lakes to temperate rivers, but not the geographical pattern presented here, from temperate to Mediterranean freshwater habitats (Fig. 3).

The decrease in fish consumption and the corresponding enlargement of the food-niche of Mediterranean otters can be related to their small body size. Ruiz-Olmo *et al.* (1998) showed that otters from temperate areas were between 35% and 11% heavier than otters inhabiting the Iberian Peninsula. Some authors (King & Moody, 1982; Clevenger, 1993) have related changes in mustelids' body size with differences in food abundance and availability. Temporally reduced fish abundance and unpredictable availability in freshwater Mediterranean environments could then favour small body sizes in otters, given that reduced energetic demands allow for a higher dietary flexibility (Gittleman & Purvis, 1998). Iriarte *et al.* (1990) also related the reduced body size of American pumas in low latitudes with broader niche breadths. Other authors (King, 1991) proved that body size in small mustelids could be linked to mean prey size. Although we do not have data on prey sizes to test this hypothesis in the case of the otter, the higher frequency of small and relatively unprofitable prey (i.e. insects) in the Mediterranean area could also be related to the otter's reduced body size.

The results of this paper show a clear dietary diversification of otters inhabiting Mediterranean freshwater ecosystems in relation with otters from temperate ones, resulting in a strong latitudinal gradient. Similar results have been published for other small and medium size predators in Mediterranean areas, and are also thought to be in response to a reduction in the diversity and abundance of their main prey (e.g. small mammals for the barn owl and the common genet; Herrera, 1974; Virgós *et al.*, 1999). This pattern cannot be extended, however, to bigger Mediterranean predators, such as the Iberian Lynx (*Lynx pardinus*

Temminck), the golden eagle (*Aquila chrysaetos* L.) (Delibes, 1975) and the badger (*Meles meles* L.) (Martín *et al.*, 1995; Goszczyński *et al.*, 2000), which in Mediterranean Iberia strongly predate upon rabbits (*Oryctogalus cuniculus*), an extremely abundant prey. Thus, the trend of increased dietary niche breadth with reduced latitude cannot be generalized to all taxa.

ACKNOWLEDGMENTS

We thank Dr B. Jędrzejewska, Dr J. Jiménez Nieva, Dr A. Rodríguez and Dr J. Calzada for their helpful comments on early versions of the manuscript. Two anonymous referees provided useful ideas and corrections. The study was financially supported by GIASA-CSIC, through the project 'Medidas compensatorias de la Autovía A-381 Jerez de la Frontera-Los Barrios'.

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APPENDIX

Otter diet composition (RFO, relative frequency of occurrence) in the thirty-seven diet studies reviewed in this paper. Prey categories are fish, crayfish, amphibians, reptiles, mammals, birds and aquatic invertebrates (excluding crayfish). Latitude and climate regime (M, Mediterranean; T, temperate) are also indicated. The references are the same as those used in Fig. 1

	Fish	Cray	Amph.	Rept.	Mamm.	Bird	Aq. Inv.	Latitude	Climate	Ref.
Portugal	25.7	54.9	9.4	0.6	–	–	9.4	38°00′	M	1
Portugal	46.6	24.8	14.5	2.1	–	1.2	12.7	37°40′	M	2
Spain	62.8	0.5	13.4	3.0	–	0.5	19.8	37°30′	M	3
Spain	67.2	–	12.5	3.1	0.3	0.3	16.7	37°00′	M	4
Spain	37.9	31.5	7.1	0.3	0.7	0.3	22.1	37°00′	M	5
Spain	62.5	–	17.1	10.1	0.2	3.6	6.4	38°30′	M	6
Spain	61.1	–	16.1	0.7	0.6	0.1	22.1	42°05′	M	7
Spain	56.6	5.6	5.2	3.3	0.3	0.5	23.1	40°30′	M	8
Spain	53.9	0.4	15.8	6.1	0.9	3.9	18.9	41°00′	M	9
Spain	57	24.5	0.5	0.9	5.1	1.3	0.4	42°45′	M	10
Spain	92.9	1.7	1.4	1.2	0.6	0.9	1.3	41°25′	M	11
Spain	59.5	35.6	3.9	3.7	–	1.3	0.9	41°00′	M	12
Italy	74.2	0.7	5.0	13.6	0.4	–	5.4	42°20′	M	13
Italy	82.7	1.8	10.2	–	1.6	2.0	1.8	40°45′	M	14
Italy	86.7	1.6	9.1	1.8	–	0.2	1.6	40°20′	M	15
Italy	75.0	5.4	12.0	2.4	–	0.2	5.4	40°10′	M	16
France	78.6	2.1	10.6	–	4.9	1.4	2.1	47°10′	T	17
France	79.0	4.2	9.7	0.6	1.5	1.1	3.9	45°40′	T	18
England	91.4	–	0.5	–	1.0	7.1	–	50°20′	T	19
England	91.8	–	0.6	–	4.2	1.1	2.3	50°30′	T	20
England	92.7	–	0.5	–	1.2	4.6	1.0	50°40′	T	21
England	71.2	–	6.8	–	0.3	4.0	17.7	51°10′	T	22
Wales	99.4	–	–	–	–	0.7	–	52°00′	T	23
Ireland	86.7	2.1	0.9	–	–	0.9	5.7	53°20′	T	24

APPENDIX *continued*

	Fish	Cray	Amph.	Rept.	Mamm.	Bird	Aq. Inv.	Latitude	Climate	Ref.
Ireland	48.1	29.1	15.0	–	–	1.9	5.5	53°40′	T	25
Ireland	89.9	–	7.4	–	0.4	0.3	2.0	54°30′	T	26
Scotland	76.0	–	19.0	–	0.7	2.9	1.4	57°30′	T	27
Scotland	93.2	–	3.1	–	1.0	–	–	57°05′	T	28
Scotland	79.9	–	16.1	–	0.4	1.8	1.8	57°05′	T	29
Denmark	85.1	–	12.5	–	0.8	1.3	0.2	56°30′	T	30
Sweden	66.9	13.5	8.0	–	0.6	9.2	1.6	55°30′	T	31
Sweden	93.4	–	1.6	–	0.1	3.9	0.9	58°01′	T	32
Germany	88.3	4.8	2.3	–	0.7	0.8	2.7	53°30′	T	33
Hungary	71.7	–	9.9	0.3	0.9	4.7	11.8	46°40′	T	34
Czech Rep.	86.0	5.5	4.0	–	2.0	2.7	5.5	49°30′	T	35
Poland	87.3	–	5.3	–	1.6	1.2	3.3	51°00′	T	36
Poland	31.4	0.4	42.8	0.4	0.8	2.4	21.6	52°45′	T	37