Diet of otters living in three different habitats in Hungary

József LANSZKI and Tamás MOLNÁR

University of Kaposvár, Faculty of Animal Science, Ecological Research Group, P.O. Box 16, H-7401 Kaposvár, Hungary; e-mail: lanszki@mail.atk.u-kaposvar.hu

Received 14 November 2002; Accepted 12 November 2003

A b s t r a c t . The seasonal diet composition of otters (*Lutra lutra*) living by an eutrophic fish pond system, a wetland alder forest, and a slow-flowing stream located in south-west Hungary was investigated by spraint analysis (n = 801, 116 and 234 samples respectively). Both percentage relative frequency of occurrence (O%) and biomass (B%) of food items (calculated by coefficients of digestibility) were estimated. The food composition of the otters living by the three areas differed significantly (P<0.001). The dominant food of the otters living by the fish pond system was fish (with 80–94 O% and 94–99 B%). The primary food source for otters living in the alder forest was fish (29–66 O%, and 47–93 B% respectively), although amphibians played a significant role during spring (31 O% and 40 B%). From autumn to spring the food sources of primary importance to otters living in the area of the stream were amphibians and reptiles (together 37–48 O% and 44–69 B%) but in summer the crayfish (*Astacus* spp.) was dominant (54 O% and 62 B%). Close correlation was found between relative frequency of occurrence and biomass of food items.

Key words: *Lutra lutra*, fish, spraint analysis, correlation, Hungary

Introduction

The feeding habits and diet composition of otters *Lutra lutra* (Linnaeus, 1758) living by ponds or on rivers has been investigated widely in regions of Europe at different geographical latitudes (e.g. E r l i n g e 1967, C h a n i n 1985, M a s o n & M a c d o n a l d 1986, C a r s s 1995, K r u u k 1995, S i d o r o v i c h 1997). Frequency of occurrence of prey remains is the most frequently used spraint analysis method (C a r s s 1995), including various means of estimation, i.e. percentage frequency of occurrence (e.g. E r l i n g e 1969, J e d r z e j e w s k a & J e d r z e j e w s k i 1998) or percentage relative frequency (e.g. E r l i n g e 1967, 1968, W i s e et al. 1981, K e m e n e s & N e c h a y 1990, W e b e r 1990, H a r n a 1993, J a c o b s e n & H a n s e n 1996, R o c h e 1998, L a n s z k i et al. 2001).

Calculation of the quantitative composition of food consumed has been performed by a number of different methods by individual authors. Thus, the results obtained can be interpreted in various ways, e.g. the score-bulk estimate (W i s e et al. 1981, J a c o b s e n & H a n s e n 1996) and the range-bulk estimate (J e n k i n s et al. 1979, J a c o b s e n & H a n s e n 1996). A further possible estimation method requires that the percentages of occurrence of various prey species are transformed into a ratio of prey biomass consumed, using the average weights of each prey item (e.g. H a r n a 1993, S i d o r o v i c h 1997, K l o s k o w s k i 1999). Although the relationship between bone size and body length or body weight can be estimated with regression analysis (W i s e 1980, C o n r o y et al. 1993, C a r s s & E l s t o n 1996, C a r s s et al. 1998, K l o s k o w s k i et al. 2000, C o p p & K o v á č 2003), the bones contained in spraints are not always appropriate for size estimation; in these cases prey size cannot be quantified. It is however possible to use multiplication factors calculated from digestibility coefficients based on feeding trials (L o c k i e 1961, F a i r l e y et al. 1987, J e d r z e j e w s k a & J e d r z e j e w s k i 1998) in the biomass ratio calculations, as with other predatory mammal species (summarised by Jedrzejewska & Jedrzejewski 1998). The percentage quantitative ratio of the food components consumed is calculated on the basis of the weight of remains identified in the otter spraints.

In Hungary (Gera 2001, Heltai 2002) and other central European countries (Kranz 2000) the otter population has been showing a tendency to increase in recent years, presumably as a result of protection and the increased development of artificial fish pond systems. The presence of the otter, particularly in those areas newly colonised, is usually accompanied by claims for estimated or actual damage. There has, however, been a relative lack of studies comparing diet around fishponds with natural or semi-natural habitats. The feeding habits of otters living by Hungarian fish ponds and some natural wetlands has been investigated on the basis of frequency of occurrence of remains in spraints (Kemenes & Nechay 1990, Lanszki & Körmendi 1996, Lanszki et al. 2001). However, the strength of the correlation between frequency data and the biomass estimation of the diet is not clear.

The objective of this study was to examine the seasonal diet composition of otters living in three different habitats applying two estimations, the percentage relative frequency of occurrence and percentage biomass, using multiplier factors.

Study Areas

Three areas, representing different habitats, were chosen for this study. The first, the Petesmalom Fish Pond System, or PFP (46°14' N, 17°29' E), is a dammed valley pond system established in continuous forest. The supplier stream forms part of the catchment system for the River Drava. Oak (*Querca* spp.) is the dominant type of forest around the ponds. These eutrophic fish ponds have an average depth of 0.7 m and a total area of 150 ha, 30% of the area being covered by reed (*Scirpo-Phragmitetum*). Fish production in the ponds in this area is extensive and is managed by a nature conservation NGO.

The second area, the Lankóci Wetland Forest or LF (46°18' N, 16°52' E), is located near to the city of Gyékényes in the Danube-Drava National Park. This area forms part of the National Biodiversity Monitoring System. The characteristic plant community of the area constantly under water is alder swamp wood (*Carici pendulae-Alnetum*). The dominant forest tree is the common alder (*Alnus glutinosa*), the characteristic bush species is grey willow scrub (*Salix cinerea*), and lesser pond sedge beds (*Carex acutiformis*) are common in the herb layer. The alder swamp woods studied are only covered by water from autumn to spring in periods of high water. The relicts of the shallow anabranches of the former rivers in this area (ox-bow lakes), forming a trench system, are also periodically covered by water (Juhász 1998). Ponds were constructed in this area (5 ha), but fish production in these ponds has now ceased. The Dombó Canal flows across the Lankóci Forest and this canal, which periodically dries up, connects with the catchment system for the River Drava. Sampling was carried out in one of the ox-bow lakes, at the abandoned ponds, along the Dombó Canal and in the alder swamp wood.

The third area was the Tetves Stream, or TS (46°44' N, 17°45' E), which runs along the border of the Látrány Puszta Nature Protection Area, near to the southern shore of Lake Balaton, among the hills in the outer area of the county of Somogy. This slow-flowing stream enters the pond system at Irmapuszta, forming part of the catchment area of Lake Balaton. In this protected area the wide sand steppe grasslands (*Astragalo-Festucetum suleatae*) of Pannonia alternate with rich fens, lowland hay meadows and small wooded areas. Field crops are characteristic on the eastern side of the stream. Samples were taken between the Látrány and Visz regions, along the stream and under bridges.

Methods

Diet composition was determined by means of spraint analysis. Spraints were collected once a month at the PFP and every six weeks at LF and TS, on a standard route (6.2 km alongside the ponds at the PFP, 2.0 km alongside the wetlands in the LF and 1.3 km along the TS). The total numbers of samples collected at the PFP (processed between December 1996 and November 1998), in the LF (between December 1999 and November 2001) and by the TS (between June 2001 and May 2002) were 801, 116 and 234 respectively.

After the spraints had been washed through filters (0.5 mm pore diameter) and dried the remains of prey items were separated. Fish species were identified from a reference collection of scales and bones, e.g. pharyngeal teeth, operculae, dentaries and maxillaries (Berinkey 1966, Knollseisen 1996, personal collection). The minimum number of fish occurring in one spraint was determined by counting characteristic bones. Other remains of food species preyed on by otters were identified from characteristic skeletal remains, teeth, hair and feathers (Jedrzejewska & Jedrzejewski 1998). Invertebrates were identified from their integuments. To calculate relative frequency of occurrence the number of occurrences recorded for the given food type was multiplied by 100, then divided by the total number of types of food identified. All dry prey remains were weighed and multiplied by coefficients of digestibility (insectivores 5, rodents 9, medium-sized mammals 25, wild boar 118, deer 15, birds 12, amphibians and reptiles 18, fish 25, molluscs and crayfish 7, insects 5, plant material 4), as summarised by Jedrzejewska & Jedrzejewski (1998), to obtain an estimate of the percentage fresh weight (biomass) of food consumed. The following food taxa were used in the trophic niche breadth calculations for each habitat: mammals, birds, reptiles, amphibians, fish, invertebrates and plant matter. Trophic niche breadth was calculated in accordance with Levin [$B = 1/\Sigma p_i^2$, where p_i = the percentage occurrence or biomass of the i^{th} taxon] (Krebs 1989).

The statistical relationship between frequency and biomass data was estimated by means of Spearman's non-parametric correlation after arc-sin transformation. The χ^2 test was applied for distribution analysis for the diet composition of the otters living in the different habitats. Analysis of variance was used to test the trophic niche breadth of the otters living in the different environments. The SPSS 7.5 statistics program (Green et al. 1997) was used to process the data obtained.

Results

Diet of otters by the fish pond system

The principle food source of the otters living by the Petesmalom Fish Pond System was fish, at 80–94% frequency of occurrence depending on season; biomass ranged between 94 and 99% (Table 1). In winter the main fish prey was the giebel carp *Carassius auratus gibelio,* the brown bullhead *Ictalurus nebulosus* being of secondary importance. Common carp *Cyprinus carpio* dominated in the diet in spring, and the fish prey species of secondary importance was again the giebel carp. In summer, the brown bullhead proved to be the most important species but pikeperch *Stizostedion lucioperca* and perch *Perca fluviatilis* also occurred in significant quantities. In autumn, the giebel carp and the common carp were most important with the brown bullhead also occurring in high quantities (Table 1).

The most frequent prey species among mammals was the water vole *Arvicola terrestris*, but the otter also preyed on other vole species (bank vole *Clethrionomys glareolus*, common vole *Microtus arvalis* and field vole *Microtus agrestis*). Less frequently, the remains of wild

Table 1. Percentage relative frequency of occurrence and percentage biomass of various fish species consumed by otters living by the Petesmalom Fish Pond System (data for two years pooled). O%: percentage relative frequency of occurrence, B%: biomass (%), +: occurring in proportions lower than 0.05%, * fish and non-fish items together.

Fish species	Petesmalom Fish Pond System							
	Winter		Spring		Summer		Autumn	
	O%	B%	O%	B%	O%	B%	O%	B%
Common carp *Cyprinus carpio*	7.0	9.2	21.5	31.1	5.5	6.0	17.2	22.6
Giebel carp *Carassius auratus gibelio*	50.4	58.1	19.6	24.3	5.5	3.0	12.1	22.8
Crucian carp *Carassius carassius*	0.9	1.3	0.8	0.9				
Carassius spp.	5.3	6.0	3.4	3.0	9.1	4.5	12.1	13.5
Bream *Abramis ballerus/A. brama*	0.1	0.1						
Rudd *Scardinius erythrophthalmus*	1.6	1.1					1.0	0.6
Silver bream *Blicca bjoerkna*	0.2	0.2			1.8	3.1		
Roach *Rutilus rutilus*	3.3	2.7	1.5	1.8			3.0	3.8
Bitterling *Rhodeus sericeus amarus*			0.3	0.2				
Stone morroco *Pseudorasbora parva*	0.9	0.2	1.3	0.4	1.8	0.3	2.0	0.7
Bleak *Alburnus alburnus*	4.0	1.2	1.0	0.9				
Asp *Aspius aspius*	0.1	0.2						
Grass carp *Ctenopharyngodon idella*	0.3	0.3	3.1	3.3	1.8	1.4	2.0	2.5
Tench *Tinca tinca*	0.1	0.2						
Chub *Leuciscus cephalus*			0.3	0.2				
Unidentified Cyprinidae	2.0	1.3	2.8	1.8	3.6	1.3	3.0	3.8
Loach *Misgurnus fossilis/Cobitis taenia*			0.6	+				
Pumpkinseed *Lepomis gibbosus*	2.5	0.9	3.4	1.1	3.6	1.2		
Perch *Perca fluviatilis*	2.7	2.7	1.3	0.7	14.5	9.6	10.1	4.5
Pike-perch *Stizostedion lucioperca*	0.1	+	1.0	0.6	7.3	9.8	2.0	1.1
Pike *Esox lucius*	0.5	0.2	5.9	7.0	1.8	0.9	2.0	1.4
Brown bullhead *Ictalurus nebulosus*	10.4	11.8	10.8	11.8	18.2	35.7	16.3	15.9
Unidentified fish	1.6	1.2	5.4	5.0	5.5	20.0	6.1	2.6
Summarized fish	94.2	98.9	84.0	94.1	80.0	96.8	88.9	95.8
No. of spraints	434		255		40		72	
Items*	754		388		55		99	

boar *Sus scrofa* (in winter), roe deer *Capreolus capreolus* (in spring) and red deer *Cervus elaphus* (in winter and spring) also occurred in the diet. Similarly, predation on birds (mainly small passerines), reptiles and amphibians reached only low levels, but amphibians had secondary importance (Table 2). Among the invertebrate species the water beetle *Dytiscus marginalis* was much in evidence. Occasional consumption of crayfish *Astacus* spp. also occurred in spring. The percentage biomass of these taxa varied at a low level, as did the biomass of plants consumed (seeds, duckweed *Lemna* spp., bullrushes *Typha* spp., sedge *Carex* spp. and gramineae Gramineae spp.; Table 2).

Diet of otters in the wetland alder forest

The dominant food source in the Lankóci Wetland Forest was also fish (Table 3), but consumption varied greatly between seasons. The biomass ratio of fish of low average weight (under 100g individual weight) reached 93%, and the most notable prey were pike *Esox lucius* and perch. The biomass ratio of fish fell below 50% in spring but in the arid summer and humid autumn periods fish consumption increased again to 72–74%. From spring to autumn the brown bullhead, the pumpkinseed (*Lepomis gibbosus*) and the perch were the most important prey species. Species which are not generally typical food sources for otters played

Table 2. Non-fish diet of otters living by Petesmalom Fish Pond System (for abbreviations see Table 1).

Fish species	Petesmalom Fish Pond System							
	Winter		Spring		Summer		Autumn	
	O%	B%	O%	B%	O%	B%	O%	B%
Water vole *Arvicola terrestris*			0.3	0.1				
Other voles Microtinae	0.5	0.3	1.1	0.4			1.0	1.4
Wild boar *Sus scrofa*	0.1	+						
Red deer *Cervus elaphus*	0.2	+	0.2	+				
Roe deer *Capreolus capreolus*			0.3	+				
Small passerines Passeriformes spp.	0.4	+	0.5	+	3.6	0.2		
Medium-sized birds			0.3	0.3				
Snakes Colubridae spp.			0.3	0.1	1.8	1.4		
Lizards Sauria spp.	0.1	+	0.3	0.1				
Anurans Anura spp.	1.4	0.6	7.2	4.6	5.5	1.2	3.0	2.7
Water beetle *Dytiscus marginalis*	0.6	+	1.1	0.1	3.7	0.3	1.0	+
Other insects Insecta spp.	1.2	+	0.8	+	1.8	+	2.0	0.1
Crayfish *Astacus* spp.			0.8	0.2				
Other invertebrates	0.3	+	0.9	0.2			4.1	+
Plants	1.1	+	2.2	+	3.6	0.1		
Summarized non-fish diet	5.9	1.1	16.3	6.0	20.0	3.2	11.1	4.2

a significant role in this area. The occurrence of small mammals was substantial from spring to autumn with biomass consumed reaching 4–7%, the water shrew *Neomys fodiens* having the greatest importance. The highest ratio of bird biomass consumed (5%) was in spring. In the forest, where available fish resources were sparse, amphibians and reptiles were the second most important food source for the otter. The predominant sources were the various species of frog (e.g. common tree frog *Hyla arborea*, other frogs *Rana* spp. and common toad *Bufo buf*o), with the ratio of biomass of this taxon reaching 36% in spring. The biomass of invertebrates

Table 3. Percentage relative frequency of occurrence and percentage biomass of various fish species consumed by otters living in the Lankóci Wetland Forest (data for two years pooled) (for abbreviations see Table 1).

Fish species	Lankóci Wetland Forest							
	Winter		Spring		Summer		Autumn	
	O%	B%	O%	B%	O%	B%	O%	B%
Giebel carp *Carassius auratus gibelio*			6.1	14.2	3.3	1.5		
Crucian carp *Carassius carassius*							2.9	3.1
Roach *Rutilus rutilus*							5.7	3.5
Gobio spp.							5.7	3.1
Stone morroco *Pseudorasbora parva*	4.9	5.9	3.1	0.9				
Tench *Tinca tinca*			1.5	0.9				
Unidentified Cyprinidae			1.5	0.8			2.9	9.2
Pumpkinseed *Lepomis gibbosus*	2.5	0.5			10.0	18.9	2.9	10.3
Perch *Perca fluviatilis*	19.5	18.8			6.7	7.5	22.8	27.0
Pike *Esox lucius*	26.8	59.1	4.6	2.5	3.3	7.5		
Brown bullhead *Ictalurus nebulosus*	9.8	8.9	6.2	17.8	16.7	31.9		
Unidentified fish	2.4	0.1	6.2	9.5	10.0	6.6	8.6	15.8
Summarized fish	65.9	93.3	29.2	46.6	50.0	73.9	51.5	72.0
No. of spraints	26		40		18		32	
Items*	41		65		30		35	

was relatively high only in spring, water beetles and water scavenger beetles Hydrophilidae spp. being the most important. Consumption of plants varied at a low level (Table 4).

Table 4. Non-fish diet of otters living in Lankóci Wetland Forest (for abbreviations see Table 1).

Food taxon	Lankóci Wetland Forest							
	Winter		Spring		Summer		Autumn	
	O%	B%	O%	B%	O%	B%	O%	B%
Insectivores Soricidae			1.5	1.0	3.3	4.3	2.9	0.4
Voles Microtinae			6.2	3.5			11.4	6.9
Small passerines Passeriformes spp.			6.2	4.5	3.3	0.7		
Medium-sized birds							2.9	2.8
Eggs			1.5	0.1				
Grass snake *Natrix natrix*			4.6	3.9				
Anurans Anura spp.	17.1	5.8	26.2	35.8	16.7	19.0	11.4	16.5
Water beetles Dytiscidae & Hydrophilidae	9.8	0.9	23.1	4.7	20.0	1.9	14.3	1.4
Other invertebrates	7.2	+	1.5	+	3.3	0.1		
Plants					3.3	0.1	5.7	+
Summarized non-fish diet	34.1	6.7	70.8	53.5	49.9	26.1	48.6	28.0

Diet of otters by the stream

In the diet of the otters living by the Tetves Stream the biomass ratio of the various species of fish varied at a low level throughout the year (17–27%), reaching a minimum in summer and a maximum in spring (Table 5). Both species characteristic of slow-flowing streams (e.g. gudgeon *Gobio gobio*) and fish ponds (e.g. common carp and silver carp *Hypophthalmichthys molitrix*) were detected.

Although amphibians played the most important role from autumn to spring (Table 6) in the diet of the otters (60% in autumn, 68% in winter and 44% in spring), in summer had only secondary importance (15%). Whilst remains of the European pond turtle *Emys orbicularis* and reptiles, e.g. grass snake *Natrix natrix,* were also found in the spraints in summer, amphibians (e.g. common tree frog, *Rana* spp. and common toad) played the determinant role. In autumn and winter, consumption of water vole reached relatively high levels (3–7%). Occurrence of birds as prey was low. The dominant prey species in summer were invertebrates (Table 6). Consumption of crayfish *Astacus* spp. was particularly important, representing 62% of the diet in summer. Their biomass was also relatively high in autumn and winter (8–9%).

The seasonal diet composition of the otters living in the different habitats varied significantly, according to both the frequency estimations (χ^2 = 75.21-454.00, df = 10, P<0.001) and the biomass estimations (χ^2 = 688.48-8348.80, df = 10, P<0.001).

Trophic niche breadth

Since the most important prey of the otter living by the Petesmalom Fish Pond system was fish, trophic niche breadth was found to be narrow. This finding was based on both frequency of occurrence (B = 1.26±0.05, mean±s.d.) and biomass estimation (B = 1.09±0.01) (Fig. 1). The value was found to be the lowest in winter (higher proportion of fish consumption) and the highest in summer, when the consumption of other prey taxa was slightly increased. The diet of otters living in the Lankóci Forest and by the Tetves Stream showed higher variability than by the fish pond system, which was also indicated by their trophic niche breadth. In the case of otters in

Table 5. Percentage relative frequency of occurrence and percentage biomass of various fish species consumed by otters living by the Tetves Stream (for abbreviations see Table 1).

Fish species	Tetves Stream							
	Winter		Spring		Summer		Autumn	
	O%	B%	O%	B%	O%	B%	O%	B%
Common carp *Cyprinus carpio*			4.4	6.9			1.4	3.9
Silver carp *Hypophthalmichthys molitrix*			1.1	1				
Giebel carp *Carassius auratus gibelio*	1.7	1.8	8.9	9.7	1.3	1.6		
Carassius spp.	0.8	1.3						
Bream *Abramis ballerus/A. brama*							2.7	3.1
Roach *Rutilus rutilus*	0.8	0.7					1.4	0.6
Gudgeon *Gobio gobio*	1.7	0.9	2.2	2.1	12.0	12.0	9.5	9.9
Stone morroco *Pseudorasbora parva*	7.6	3.6			0.6	0.7	1.4	1.1
Bleak *Alburnus alburnus*	4.2	2.7	3.3	3.0	1.3	0.2		
Unidentified Cyprinidae	0.8	0.4	3.3	3.4	1.3	0.2		
Loach *Misgurnus fossilis/Cobitis taenia*					0.6	+		
Pumpkinseed *Lepomis gibbosus*	1.7	0.8			0.6	0.3		
Perch *Perca fluviatilis*			1.1	+				
Pike *Esox lucius*							1.4	0.1
Brown bullhead *Ictalurus nebulosus*					0.6	0.4		
Unidentified fish	2.5	6.8	3.3	0.6	1.3	1.0	2.8	4.1
Summarized fish	21.8	18.9	27.8	26.8	20.1	16.7	20.6	22.8
No. of spraints	58		61		34		81	
Items*	119		90		73		154	

the Lankóci Wetland Forest, the wider trophic niche was found to be related to frequency of occurrence (B = 2.99±0.14), the breadth being relatively narrow based on biomass estimation (B = 1.73±0.09, Fig. 1). The narrowest trophic niche breadth was found in winter (with a higher proportion of fish consumption), while the index was almost doubled in spring when the role of other prey taxa (mainly amphibians) in the diet of otter become more important. By the Tetves Stream the trophic niche breadth of otters was found to be high on the basis of both frequency of occurrence (B = 3.00±0.06) and biomass estimation (B = 2.67±0.35, Fig. 1). The narrowest food niche was observed in summer, in the season when great quantities of crayfish were consumed.

Frequency of occurrence among the diet components revealed that the food niche of the

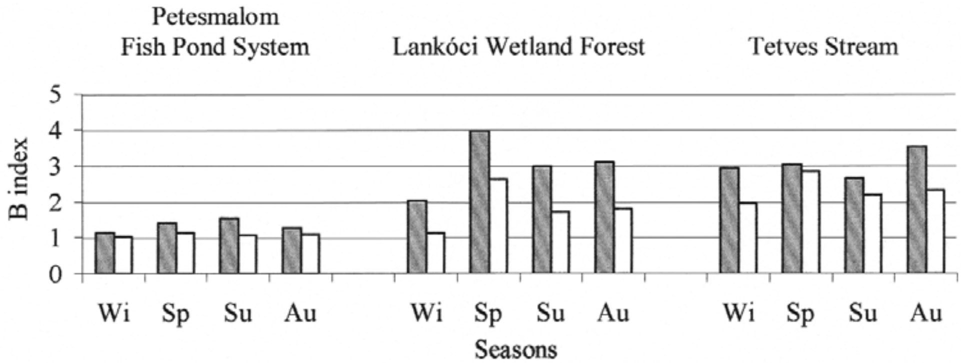

Fig. 1. Trophic niche breadth (B) of otters living in three different habitats in Hungary estimated by frequency of occurrence (shaded bars) and biomass (open bars). Seasons: Wi – winter, Sp – spring, Su – summer, Au – autumn.

Table 6. Non-fish diet of otters living by the Tetves Stream (for abbreviations see Table 1).

Fish species	Tetves Stream							
	Winter		Spring		Summer		Autumn	
	O%	B%	O%	B%	O%	B%	O%	B%
Insectivores Soricidae	0.8	0.6						
Water vole *Arvicola terrestris*	2.4	3.2					12.3	6.9
Other voles Microtinae			1.1	+	1.3	+		
Pheasant *Phasianus colchicus*	0.8	0.8						
Small passerines Passeriformes spp.	0.8	0.1			0.6	0.1		
European pond turtle *Emys orbicularis*					1.9	2.1		
Other reptiles Reptilia spp.					1.9	4.4		
Anurans Anura spp.	47.6	68.5	36.7	44.3	15.8	14.9	37.0	60.4
Water beetles Dytiscidae & Hydrophilidae	1.6	+	1.1	+	2.5	+	4.2	+
Crayfish *Astacus* spp.	22.6	7.8	33.3	28.9	47.5	61.6	13.6	8.6
Other invertebrates	0.8	+			4.5	0.1	12.3	1.3
Plants					3.9	+		
Summarized non-fish diet	77.4	81.1	72.2	73.2	79.9	83.3	79.4	77.2

otters living by the fishpond was significantly ($P<0.001$) narrower than that of those living in the forest or by the stream. The latter two groups proved not to differ significantly from each other with respect to food niche. The biomass calculations showed substantial difference between the niche breadths of the otters living in the three areas ($P<0.001$).

Relationship between estimated frequency of occurrence and biomass

The percentage biomass of fish was 5–17% higher in the Petesmalom Fish Pond system and 21–27% in the Lankóci Forest (summarized fish, Tables 1 and 3) than the corresponding relative frequencies of occurrence. By the Tetves Stream this difference was found to be between +2 and -3% for fish prey (summarized fish, Table 5). The biomass data were lower than the occurrence figures for the other taxa. The Spearman's correlations between occurrence and biomass value for the various taxa were as follows: mammals: $r = 0.82$, ($P<0.01$), birds: $r = 0.91$ ($P<0.001$), reptiles and amphibians: $r = 0.90$ ($P<0.001$), fish: $r = 0.97$ ($P<0.001$), invertebrates: $r = 0.91$ ($P<0.001$) and plants: $r = 0.97$ ($P<0.001$).

Discussion

On the basis of this study we ascertained that there was a substantial difference between the diet composition of the otters living in the fishpond system and that of those living in natural or near-natural habitats. The habitat-dependent, highly varied food niche breadth values obtained (B = 1-4) signify that the otter is capable of adapting well to substantially different, and in some cases, extreme conditions. This could be significant primarily with regard to the conservation of Central European aqueous habitats or their possible renovation.

Fish are generally the main food source for the otter (e.g. Erlinge 1967, Wise et al. 1981, Mason & Macdonald 1986, Carss 1995, Kruuk 1995), but the fishpond system was the only area included in this study in which fish constituted a food source of primary importance in every season. In this habitat it was found, particularly with respect to the biomass proportions of the food sources, that the otter consumed almost exclusively fish. Similar results have been obtained at other eutrophic fish ponds in Hungary (Kemenes & Nechay 1990, Lanszki et al. 2001), but with greater seasonal fluctuations. It is a point worthy of note with respect to pond management that, of the fish species available in winter (common carp and giebel carp), the otter tended to consume primarily the smaller and less economically important giebel carp.

Non-typical diet components, such as wild boar, roe deer and red deer or plant, occurred in the diet of the otters living by the fishponds surrounded by forest. It may be assumed that these had been left in the vicinity of the water after being shot during hunting. Similar observations have been made in several other instances (e. g. Roche 1998, Lanszki et al. 2001). In this study it was found that the otters consumed very little carrion, as indicated by the extremely small quantities of carrion food remains identified. The remains of the plants listed in Tables 2, 4 and 6 passed through the digestive system of the otters. It is difficult to determine on an individual basis subsequent to the study whether the otters ingested these directly (which is probable in the case of bullrush, plants of the sedge family and those of the grass family Gramineae) or together with their prey (the probable explanation for the occurrence of duckweed). It was found that the otters consumed only negligible proportions of these species. In some other areas, extremely small percentages of plant consumption have been reported (e.g. Roche 1998, Wise et al. 1981).

Fish proved less important in the diet of the otters living in the alder forest than for those living in the fishpond system. The canal flowing through the forest connects intermittently with the River Drava, however there was no fish stock management; this was corroborated by the species composition of the fish component of the otters' diet. Rarer fish species, inhabiting stagnant waters which are gradually becoming terrestrialised (e.g. tench *Tinca tinca*), and fish living in slow-flowing streams (e.g. gudgeon *Gobio* spp.) both occurred as prey. However, it was the species with greater ecological tolerance, commonly found mainly in shallow stagnant waters (such as pike and pumpkinseed) which were the main food source for the otters.

The otters presumably ventured into larger areas (alder forests, canals and stagnant ponds) to search for food; evidence for this was that the non-fish component of their diet, including mammals (especially insectivores), birds and amphibians, played a significant role. It was particularly in spring that the otters consumed amphibians (primarily frog species) in large quantities. Consumption of amphibians is substantially dependent on the stocks available (Erlinge 1967, Weber 1990), but consumption of high ratios of hibernating and spawning amphibians has been observed at different geographical latitudes (Erlinge 1967, Chanin 1985, Weber 1990, Sidorovich 1997, Roche 1998, Lanszki et al. 2001). In habitats in the temperate climate of Central Europe amphibians generally play a role of secondary importance beside the dominant fish (Kemenes & Nechay 1990, Lanszki et al. 2001).

Slow-flowing streams with a low flowrate (particularly in summer), wedged between areas of arable land and meadows and often feeding fishponds, are typical of the Southern Transdanubian region. The stream featured in this study also has these characteristics and otters occurred there continuously. The particular characteristic of this area is that two species of crayfish (*Astacus leptodactylus* and *A. astacus*) inhabit the stream intermittently in high densities. This study found that the two crayfish species accounted for a high proportion of the diet of the otter in summer, when they were the principle food source.
A high level of predation on crayfish by otters living by a stream has also been recorded in summer by Erlinge (1967) in Sweden, McFadden & Fairley (1984) in Ireland and Sidorovich (1997) in Belarus; however, this has rarely been found to occur in other

seasons. Other studies (e.g. Taastrøm & Jacobsen 1999) have reported consumption of these species which was, at most, at a low level. From autumn to spring amphibians were the primary food source for the otter, taking the place of the two species of crayfish, while the various fish species played a subordinate role in the diet throughout the year.

European pond turtle was found to inhabit all the three areas studied but consumption of this species was recorded in only three instances; all these were by the otters living by the stream. As the thin external lamella of the carapace was detected in the spraints, direct predation cannot be ruled out. We have observed (unpublished data) direct predation on turtles in other areas, but no case of otters chewing the carapace has been recorded. However, in this case it may be that the otters ate the carcasses of animals which were already dead (perhaps hit by vehicles) and mutilated.

Spraint analyses based on the calculation of frequency of occurrence in the diet have their limitations (detailed by Carss 1995, Carss & Parkinson 1996). It was for this reason that, in this study, in addition to calculation of relative frequency of occurrence, a biomass calculation method suitable for practical application (Jedrzejewska & Jedrzejewski 1998) was used. The close correlation values obtained indicated that it is possible to draw conclusions on the quantitative ratios of the food source from data for percentage relative frequency of occurrence, although there may be differences depending on the characteristics of the area in question (or rather, depending on whether fish play a primary or secondary role in the diet). Generally, biomass estimates for fish prey were higher than the corresponding relative frequencies of occurrence, but for non-fish prey, the situation was reversed.

The biomass calculation method applied in this study used the weight of the food remains found in the spraints as the basis for calculations; this was independent of the determination of the size of the prey species and any inaccuracy thereof. The method used in this study is not suitable for determination of the absolute quantity of food matter consumed (which, indeed, is not possible with the other methods either); its purpose is merely to ascertain the quantitative ratio of the food elements consumed in relation to each other. This method is widely applied for other predatory species, with different correction factors (summarized by Jedrzejewska & Jedrzejewski 1998); it could also represent a methodology suitable for application in otter studies.

Acknowledgements

We are grateful to D.L. Moss and to A. Szabó for their help in the English proofreading and also the two anonymous referees for advice in the composition of the manuscript. This work was supported by the Hungarian Fund for Scientific Research (OTKA no. F 023057, F 037557) and the Bolyai scholarship. Biomonitoring on the Drava River was co-ordinated by the Danube-Drava National Park.

LITERATURE

BERINKEY L. 1966: Halak - Pisces. *Akadémia Press, Budapest* (*in Hungarian*).

CARSS D.N. 1995: Foraging behaviour and feeding ecology of the otter *Lutra lutra*: a selective review. *Hystrix 7: 179–194.*

CARSS D.N. & ELSTON D.A. 1996: Errors associated with otter *Lutra lutra* faecal analysis. II. Estimating prey size distribution from bones recovered in spraints. *J. Zool (Lond.) 238: 319–332.*

CARSS D.N. & PARKINSON S.G. 1996: Errors associated with otter *Lutra lutra* faecal analysis. I. Assessing general diet from spraints. *J. Zool (Lond.) 238: 301–317.*

CARSS D.N., ELSTON D.A. & MORLEY H.S. 1998: The effects of otter *Lutra lutra* activity on spraint production and composition: implications for models which estimate prey-size distribution. *J. Zool. (Lond.) 244: 295–302.*

CHANIN P.R.F. 1985: The natural history of otters. *Croom Helm., London.*

CONROY J.W.H., WATT J, WEBB J.B. & JONES A. 1993: A guide to identification of prey remains in otter spraint. Occasional Publication No. 16. *The Mammal Society, London.*
COPP G.H. & KOVÁČ V. 2003: Biometric relationships between body size and bone lengths in fish prey of the Eurasian otter *Lutra lutra*: chub *Leuciscus cephalus* and perch *Perca fluviatilis*. *Folia Zool. 52: 109–112.*
ERLINGE S. 1967: Food habits of the fish-otter *Lutra lutra* L. in South Swedish habitats. *Viltrevy 4: 371–443.*
ERLINGE S. 1968: Food studies on captive otters *Lutra lutra* L. *Oikos 19: 259–270.*
ERLINGE S. 1969: Food habits of the otter *Lutra lutra* L. and the mink *Mustela vison* Schreber in a trout water in southern Sweden. *Oikos 20: 1–7.*
FAIRLEY J.S., WARD D.P. & SMAL C.M. 1987: Correction factors and mink faeces. *Ir. Nat. J. 22: 334–336.*
GERA P. 2001: [Comprehensive report on survey of the otter *Lutra lutra* Linnaeus, 1758 between 1995–2001]. *Foundation For Otters. Budapest* (*in Hungarian*).
GREEN S.B., SALKIND N.J. & AKEY T.M. 1997: Using SPSS for Windows: analyzing and understanding data. *Prentice Hall, New Jersey.*
HARNA G. 1993: Diet composition of the otter *Lutra lutra* in the Bieszczady Mountains, south-east Poland. *Acta Theriol. 38 (2) 167–174.*
HELTAI M. 2002: The status and distribution of mammal predators in Hungary. *Doctoral thesis, St. Stephen University, Gödöllő, Hungary*.
JACOBSEN L. & HANSEN H.-M. 1996: Analysis of otter *Lutra lutra* spraints: Part 1: Comparison of methods to estimate prey proportions; Part 2: Estimation of the size of prey fish. *J. Zool (Lond.) 238: 167–180.*
JEDRZEJEWSKA B. & JEDRZEJEWSKI W. 1998: Predation in vertebrate communities. The Bialowieza Primeval Forest as a Case Study. *Springer-Verlag, Berlin Heidelberg, New York.*
JENKINS D., WALKER J.G.K. & MCCOWAN D. 1979: Analyses of otter *Lutra luta* faeces from Deeside, N.E. Scotland. *J. Zool. (Lond.) 187: 235–244.*
JUHÁSZ M. 1998: [Detailed botanical survey on the area of the Danube Drava National Park. Division of the county Somogy 3. Lankóci Forest]. *Bulletin, Museum of County Somogy, Kaposvár* (*in Hungarian*).
KEMENES K.I. & NECHAY G. 1990: The food of otters *Lutra lutra* in different habitats in Hungary. *Acta Theriol. 35: 17–24.*
KLOSKOWSKI J. 1999: Otter *Lutra lutra* predation in cyprinid-dominated habitats. *Z. Säugetierkd. 64: 201–209.*
KLOSKOWSKI J., GRENDEL A. & WRONKA M. 2000: The use of fish bones of three farm fish species in diet analysis of the Eurasian otter, *Lutra lutra*. *Folia Zool. 49: 183–190.*
KNOLLSEISEN M. 1996: Fischbestimmungsatlas, als Grundlage für nahrungsökologische Untersuchungen. *Boku-Reports on Wildlife Research and Game Management, Wien.*
KRANZ A. 2000: Otters *Lutra lutra* increasing in Central Europe: from the threat of extinction to locally perceived overpopulation? *Mammalia 64: 357–368.*
KREBS C.J. 1989: Ecological methodology. *Harper Collins Publishers, New York.*
KRUUK H. 1995: Wild otters. Predation and population. *Oxford University Press, Oxford.*
LANSZKI J. & KÖRMENDI S. 1996: Otter diet in relation to fish availability in a fish pond in Hungary. *Acta Theriol. 41: 127–136.*
LANSZKI J., KÖRMENDI S., HANCZ C. & MARTIN T.G. 2001: Examination of some factors affecting selection of fish prey by otters *Lutra lutra* living by eutrophic fish ponds. *J. Zool. (Lond.) 255: 97–103.*
LOCKIE J.D. 1961: The food of the pine marten *Martes martes* in West Ross Shire, Scotland. *Proc. Zool. Soc. Lond. 136: 187–195.*
MASON C.F. & MACDONALD S.M. 1986: Otters: ecology and conservation. *Cambridge Univ. Press, Oxford.*
McFADDEN Y.M.T. & FAIRLEY J.S. 1984: Food of otters *Lutra lutra* L. in an Irish limestone river system with special reference to the crayfish *Austropotamobius pallipes* (Lereboullet). *J. Life Sciences R. Dubl. Soc. 5: 65–76.*
ROCHE, K. 1998: The diet of otters. In: Dulfer R. & Roche K. (eds), First phase report of the Trebon otter project. Scientific background and recommendations for conservation and management planning. *Nature and environment, no. 93, Council of Europe Publishing, Strasbourg: 57–71*.
SIDOROVICH V. 1997: Mustelids in Belarus. *Zolotoy uley publisher, Minsk.*
TAASTRØM H.-M. & JACOBSEN L. 1999: The diet of otters (*Lutra lutra* L.) in Danish freshwater habitats: comparison of prey fish populations. *J. Zool. (Lond.) 248: 1–13.*
WEBER J.-M. 1990: Seasonal exploitation of amphibians by otters *Lutra lutra* in north-east Scotland. *J. Zool. (Lond.) 220: 641–651.*
WISE M.H. 1980: The use of fish vertebrae in scats for estimating prey size of otters and mink. *J. Zool. (Lond.) 192: 25–31.*
WISE M.H., LINN I.J. & KENNEDY C.R. 1981: A comparison of the feeding biology of mink *Mustela vison* and otter *Lutra lutra. J. Zool. (Lond.) 195: 181–213.*