DIET COMPOSITION OF OTTERS (LUTRA LUTRA L.) LIVING ON SMALL WATERCOURSES IN SOUTHWESTERN HUNGARY

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The diet composition of Eurasian otters (Lutra lutra) was studied by spraint (faecal) analysis (n = 1,460 samples), over a two-year period, on five sections of stream and channel in the Dráva region of southwest Hungary. The primary food of otters was generally fish (range: 33.3–89.9%, biomass estimation), with amphibians of secondary importance (3.4–48.5%). Highest fish consumption was found in winter and lowest in spring. Amphibians were eaten more in spring than in winter. Mammals (range 2.0–9.3%), birds (1.1–4.1%), reptiles (up to 22.2%), crayfish (up to 1.7%) and insects (0.1–4.2%) were consumed at low levels. Trophic niche breadth did not differ significantly between areas, though the widest and lowest seasonal values differed greatly (summer B = 2.48, winter B = 1.12). Otters preyed mainly on small fish (< 100 g in weight, range 88.0–96.9% biomass) at all study areas. Eurytopic (mean 72.7%) and stagnophilic fish (mean 21.7%) were taken preferentially, with lesser consumption of reophilic species (mean 5.6%). Non-native fish were taken most often (mean 71.0%, e.g. gibel carp, brown bullhead). Our results indicate that small watercourses can play an important role as regards otter habitat and, as such, should receive more attention when assessing habitats for otter.

Key words: Lutra lutra, food, stream, channel, non-native fish

INTRODUCTION

The Eurasian otter Lutra lutra (LINNAEUS, 1758) can potentially inhabit a wide variety of wetland habitats in Europe (CONROY & CHANIN 2002), provided the fish supply is sufficient (KRUUK et al. 1991) and waterside vegetation gives sufficient cover (ERLINGE 1967, KEMENES & DEMETER 1995). In the moderate climate Pannonian biogeographical region, the most important otter habitats are ponds, backwaters and rivers as fish are generally available throughout the year in these areas. Reedbeds, shrubs and waterside forests usually surround such areas, all representing suitable habitat for otters. In autumn fishponds are drained to harvest the fish stock and so in winter this means a drop in prey availability. Furthermore, ice can make many ponds and rivers innaccessible to otters (e.g. KRANZ 2000), and this again results in a lack of prey. Just as with summer droughts, as in the Mediterranean region (e.g. RUIZ-OLMO et al. 2002), this can make otters temporarily shift their home ranges (or share them) at this time. Streams and channels
connecting main otter habitats are important for the migration of otters (LANSZKI et al. 2008a) and also as potential feeding areas in their own right. In areas where food supply is insufficient, however, or where rivers dry up periodically or watershed vegetation is sparse, otter signs may be found only occasionally (DELIBES et al. 2000, RUIZ-OLMO et al. 2001, 2002, LANSZKI & SZÉLES 2006). These ecological conditions are typical for the regulated streams and artificial channels in the Dráva region of Hungary.

The diet of otters living on smaller streams and channels has been studied less in comparison with that from other important European habitats of the species such as coastal areas, small and large rivers (JEDRZEJEWSKA et al. 2001, CLAVERO et al. 2003). Data for small watercourses are available from cold (or temperate) zone (Sweden: ERLINGE 1967, Scotland: WEBER 1990, Poland: HARNA 1993, Belarus: SIDOROVICH 1997) and from Mediterranean countries (Portugal: BEJA 1996, Spain: RUIZ-OLMO et al. 2002, CLAVERO et al. 2005, Greece: GOURVELOU et al. 2000). In these studies, the primary food of otters consisted of species living in or near the water, such as fish, crayfish and amphibians, and otters also preyed on insects, birds and small mammals. In Hungary, otter diet composition from small watercourses is known only from a stream (LANSZKI & MOLNÁR 2003) near Lake Balaton. There is, therefore, relatively little information about the feeding habits of otters living on small watercourses in the Pannonian biogeographic region. At the same time, small watercourses, which are threatened by successive droughts which are resulting in an overall drying out of the area, and by canalization and/or drainage may play an important role in otter conservation.

The aim of this study was to evaluate area- and season-dependent variations in feeding habits of otters living on five sections of stream and channel in agro-ecosystems of the Drava region of south-western Hungary helping the conservation of the otter.

MATERIAL AND METHODS

Study areas

In the catchment of the Drava River (as with other rivers) in the last centuries the streams were regulated (by dredging the streambed, cutting the meanders) and the drainage has been altered with canalization and reclamation to allow more agriculture. Five small, regulated sections of streams and channels were examined in the Dráva region of south-western Hungary (W1 – Dombó-channel, near to Gyékényes; W2 – Dombó-channel, near to Berzence; W3 – Babócsai stream, near to Babócsa; W4 – Barcs-Komlósdi stream, near to Barcs-Drávaszentes and W5 – Korcsina channel, near to Lakócsa; from W1: 46°02’N, 17°21’E to W5: 45°54’N, 17°42’E; Fig. 1). Mean discharge of the 1–2 m wide and 0.5 m deep Dombó-channel is 1.0 m³/s (min-max: 0–9.4 m³/s), the 2.5–3.0 m wide and 0.5 m deep Babócsai stream is 3.7 m³/s (min-max: 0.06–43.5 m³/s), the 1.5 m wide and 0.3–0.5 m deep Barcs-
Komlósdi stream is 0.33 m³/s (min-max: 0.02–1.7 m³/s) and the 3–4 m wide and 0.5–1.0 m deep Korcsina channel is 0.40 m³/s (min-max: 0–2.2 m³/s). Beds of the watercourses are composed of natural soil. All banks of the streams and channels are typically agricultural in character. The watercourses are adjacent to wood patches, but the vegetation of the banks are characteristically sparse. Thin willows with reeds, or grassy strips divide the streambed from ploughed farmlands or grazing pastures. Near the studied five sections of watercourses there are no stagnant waters (within 1.4, 1.9, 3.3, 2.3 and 5.3 km, respectively), and human use (abstraction) of the water supply is inconsiderable.

Sample collection and diet analysis

Diet composition was determined by spraint (faecal) analysis. Individual spraint samples (each correspond to one spraint) were collected monthly from June 2002 to May 2004 at or close to bridges (n = 254 (W1), 470 (W2), 308 (W3), 327 (W4), and 101 (W5) spraints; for seasonal distribution of spraints see Fig. 2). Spraints were soaked in water and then washed through a 0.5 mm sieve and dried in room temperature. All recognisable prey remains were separated. The remains were ex-
examined under a microscope and fish species identified based on the morphological differences of scales and bones, e.g. pharyngeal teeth, operculae, dentaries, maxillaries (e.g. BERINKEY 1966, KNOLLSEISEN, 1996; and personal collection). Both amphibians and fish have single and paired bone structures around the head that allow an assessment of the minimum number of individuals in a spraint through the pairing of left and right sided bones of the same size. Different fish bones combined with scale characters were used to distinguish and identify fish species (and weight categories) in order to avoid overestimating the importance of the given fish taxa (CARSS & NELSON 1998). The estimation of actual biomass consumed (detailed below) provides a more realistic measurement of the nutritive value of a prey, emphasizing the importance of larger prey. Weight category was recorded on the basis of comparative measurement of the available pharyngeal teeth, operculae, preopercule, maxillaries, vertebrae or other fish bones from the spraint and using a reference collection. Fish individuals were divided into the following categories: < 100 g, 100–500 g, 500–1000 g and > 1000 g (LANSZKI & SALLAI 2006). The characteristic habitat of the various fish species within the water body were categorised according to SALLAI (2002) and LANSZKI & SALLAI (2006) as follows: reophilic (characteristically flow preferring), eurytopic (tolerant of both rivers and standing waters) and stagnophilic (characteristically preferring stagnant waters). The fish species on the basis of their autochthonism were also categorised into native and non-native species according to SALLAI (2002). Other prey species preyed upon by otters were identified by microscope from characteristic skeletal remains, teeth, hair, feathers and integuments (MÄRZ 1972, BROWN et al. 1993, KNOLLSEISEN 1996, and reference collections). All dried prey remains for each prey group recovered from spraints were weighed and their weight multiplied by an appropriate coefficient of digestibility (insectivores – 5, rodents – 9, birds – 12, amphibians and reptiles – 18, fish – 25, molluscs and crayfish – 7, insects – 5 and plants – 4; summarised in JEDRZEJEWSKA & JEDRZEJEWSKI 1998) to obtain an estimate of the percentage fresh weight of food consumed (%B).

Statistical analysis

The following six main prey taxa were used in the calculations: 1 – mammals, 2 – birds, 3 – reptiles, 4 – amphibians, 5 – fish and 6 – invertebrates. Spearman’s non-parametric correlation was used to test the statistical relationship between seasonal mean number of individuals and biomass of main food taxa. Trophic niche breadth (B index) was calculated using $B = 1/\sum p_i^2$, where $p_i$ is the proportion of the biomass of a given taxon (expressed as a percentage) present in the diet (see KREBS 1989).

The Chi-squared ($\chi^2$) test was used for distribution analysis of diet composition (six main prey categories) of the otters living in the various habitats, and year-dependent analysis of diet. Two-way analysis of variance (MANOVA, GLM procedure, fix factors: area and season, LSD post-hoc test) was applied for the evaluation of the consumption of six main food taxa, and trophic niche breadth values between areas and seasons. The SPSS (1999) statistical package was used for the processing of the data obtained.

RESULTS

Food pattern and trophic niche breadth

A strong correlation was found between mean number of individuals and biomass of main food taxa (Table 1) and, therefore, percentage biomass data were
used in the detailed evaluation. The results of two years’ dietary data were combined as there was no significant difference between the first and second year in consumption of main food categories such as fish (paired samples t-test, $t_3 = 0.10–1.68$, $P = 0.192–0.912$), and amphibians ($t_3 = 0.55–1.49$, $P = 0.233–0.618$), and also as no significant difference was found between years in the B indices ($t_3 = 0.14–3.14$, $P = 0.052–0.899$).

The principal prey of otters was generally fish in all the areas studied (range – W1: 15.8–95.5, W2: 63.7–98.0, W3: 51.6–100, W4: 25.4–99.6 and W5: 20.5–95.0; Fig. 2; Table 2). The diet of otters living on the different watercourses varied sig-

**Table 1.** Correlation between number of occurrence and biomass of main food taxa in the diet of otters in small watercourses of the Dráva region, Hungary.

<table>
<thead>
<tr>
<th>Fish</th>
<th>Amphibians</th>
<th>Reptiles</th>
<th>Mammals</th>
<th>Birds</th>
<th>Invertebrates</th>
<th>Plants</th>
</tr>
</thead>
<tbody>
<tr>
<td>$r_s$</td>
<td>0.901</td>
<td>0.763</td>
<td>0.983</td>
<td>0.766</td>
<td>0.794</td>
<td>0.569</td>
</tr>
<tr>
<td>$n$</td>
<td>20</td>
<td>20</td>
<td>20</td>
<td>18</td>
<td>16</td>
<td>20</td>
</tr>
<tr>
<td>$P &lt;$</td>
<td>0.001</td>
<td>0.001</td>
<td>0.001</td>
<td>0.001</td>
<td>0.001</td>
<td>0.01</td>
</tr>
</tbody>
</table>

Fig. 2. The diet pattern of otters living by streams and channels in the Dráva region. For locations (W1–5) see Fig. 1, n = number of spraint samples.
Table 2. Annual fish diet of otters living by streams and channels in the Dráva region, Hungary. For abbreviations: + = biomass less than 0.05%; for locations abbreviations (W1–5) see Fig. 1. Pooled data for two years (June 2002 to May 2004), N = number of items, %B = percentage biomass of each prey species consumed. Empty cells mean that the given taxon was not detected. Fish guilds: RE – reophilic or flow preferring, EU – eurytopic or tolerant for rivers and stagnant waters, and ST – stagnophilic or stagnant water preferring.

<table>
<thead>
<tr>
<th>Fish taxon</th>
<th>Fish guild</th>
<th>W1</th>
<th>%B</th>
<th>W2</th>
<th>%B</th>
<th>W3</th>
<th>%B</th>
<th>W4</th>
<th>%B</th>
<th>W5</th>
<th>%B</th>
<th>N</th>
<th>%B</th>
</tr>
</thead>
<tbody>
<tr>
<td>Common carp</td>
<td>EU</td>
<td>1</td>
<td>1.1</td>
<td>3</td>
<td>0.8</td>
<td>3</td>
<td>0.8</td>
<td>8</td>
<td>1.6</td>
<td>44</td>
<td>50.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carassius spp.</td>
<td>EU</td>
<td>12</td>
<td>2.2</td>
<td>88</td>
<td>17.3</td>
<td>200</td>
<td>49.4</td>
<td>224</td>
<td>65.0</td>
<td>1</td>
<td>0.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rudd Scardinius erythrophthalmus</td>
<td>ST</td>
<td>6</td>
<td>1.9</td>
<td>18</td>
<td>3.0</td>
<td>4</td>
<td>2.0</td>
<td>4</td>
<td>1.3</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bream Abramis ballerus/A. brama</td>
<td>RE</td>
<td>2</td>
<td>0.4</td>
<td>1</td>
<td>0.3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chub Leuciscus cephalus</td>
<td>RE</td>
<td>5</td>
<td>1.3</td>
<td>4</td>
<td>0.6</td>
<td>1</td>
<td>0.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Barbel Barbus barbus</td>
<td>RE</td>
<td></td>
<td></td>
<td>2</td>
<td>0.6</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Roach Rutilus rutilus</td>
<td>EU</td>
<td>3</td>
<td>0.7</td>
<td>17</td>
<td>2.5</td>
<td>15</td>
<td>3.2</td>
<td>1</td>
<td>0.2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bitterling Rhodeus sericeus amarus</td>
<td>EU</td>
<td>12</td>
<td>1.5</td>
<td></td>
<td></td>
<td>2</td>
<td>+</td>
<td>1</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bleak Alburnus alburnus</td>
<td>EU</td>
<td>17</td>
<td>3.1</td>
<td>22</td>
<td>2.7</td>
<td>6</td>
<td>1.3</td>
<td>5</td>
<td>1.0</td>
<td>7</td>
<td>1.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stone morroco Pseudorasbora parva</td>
<td>ST</td>
<td>4</td>
<td>1.0</td>
<td>31</td>
<td>4.0</td>
<td>4</td>
<td>0.2</td>
<td>179</td>
<td>7.7</td>
<td>2</td>
<td>1.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grass carp Ctenopharyngodon idella</td>
<td>EU</td>
<td></td>
<td></td>
<td>9</td>
<td>1.7</td>
<td></td>
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<td>11</td>
<td>5.3</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gobio spp.</td>
<td>RE</td>
<td>30</td>
<td>8.0</td>
<td></td>
<td></td>
<td>2</td>
<td>0.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tench Tinca tinca</td>
<td>ST</td>
<td>2</td>
<td>1.2</td>
<td>1</td>
<td>0.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unidentified cyprinids</td>
<td></td>
<td>7</td>
<td>0.7</td>
<td>19</td>
<td>1.7</td>
<td>5</td>
<td>0.5</td>
<td>9</td>
<td>0.4</td>
<td>1</td>
<td>0.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Loach Misgurnus fossilis/ Cobitis taenia</td>
<td>ST</td>
<td>1</td>
<td>0.5</td>
<td></td>
<td></td>
<td>2</td>
<td>0.3</td>
<td>1</td>
<td>0.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brown bullhead Ameiurus nebulosus</td>
<td>ST</td>
<td>15</td>
<td>3.2</td>
<td>174</td>
<td>31.0</td>
<td>56</td>
<td>10.1</td>
<td>29</td>
<td>4.5</td>
<td>7</td>
<td>5.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pumpkinseed Lepomis gibbosus</td>
<td>EU</td>
<td>24</td>
<td>3.3</td>
<td>47</td>
<td>6.4</td>
<td>45</td>
<td>7.2</td>
<td>7</td>
<td>0.8</td>
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<tr>
<td>Perch Perca fluviatilis</td>
<td>EU</td>
<td>8</td>
<td>1.7</td>
<td>72</td>
<td>8.2</td>
<td>62</td>
<td>6.6</td>
<td>4</td>
<td>0.2</td>
<td>2</td>
<td>1.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pike Esox lucius</td>
<td>EU</td>
<td>5</td>
<td>1.1</td>
<td>22</td>
<td>2.5</td>
<td>7</td>
<td>1.5</td>
<td>5</td>
<td>1.1</td>
<td>7</td>
<td>5.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unidentified fish</td>
<td></td>
<td>24</td>
<td>2.1</td>
<td>28</td>
<td>1.4</td>
<td>25</td>
<td>1.6</td>
<td>5</td>
<td>0.4</td>
<td>5</td>
<td>0.5</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
nificantly (Chi-Square test, $\chi^2_{20} = 343.71$, $P < 0.001$). Area-dependent differences arose mainly from the dissimilarity in consumption of fish (MANOVA, $F_{3,4} = 6.90$, $P < 0.01$), and amphibians ($F_{3,4} = 18.33$, $P < 0.001$), the main secondary food source. Otters living at W1 consumed significantly less fish, and more amphibians and reptiles, than those living in the other areas. No area-dependent difference was found in consumption of mammals, invertebrates and plant matter ($P = 0.15–0.73$). Highest fish consumption was observed in the winter and the lowest in spring ($F_{3,4} = 15.59$, $P < 0.001$; Fig. 2). The role of the non-fish component of the diet was considerable in spring and summer (Fig. 2), significantly more amphibians being eaten by otters in spring than in winter, depending on area ($F_{3,4} = 26.78$, $P < 0.001$). Otters fed mainly on *Carassius* spp. (especially giebel carp *Carassius auratus gibelio*) at W4 and W5, *Carassius* spp. and *Gobio* spp. at W3, and brown bullhead *Ameiurus nebulosus* at W2. Among amphibians, mainly frogs *Anura* spp. were eaten, especially at W1 and W5, and rarely toad *Bufo* spp. and tree frog *Hyla arborea*. Remains of European pond turtle *Emys orbicularis* were found in two spraints in summer at area W2. Among birds, mainly waterfowl (e.g., anserines) and rarely small passerines (especially in summer at W3 and W4) or pheasant *Phasianus colchicus* were consumed. Small mammal prey consisted mainly of water vole *Arvicola terrestris* (especially at W1 and W2) and muskrat *Ondatra zibethicus* (W1, W2, W3), with *Microtus* spp. and field mouse *Apodemus* spp., brown rat *Rattus norvegicus* (W2) and insectivores (e.g. water shrew *Neomys* spp.) taken rarely. Invertebrates such as *Austacus* spp. (at W2, W3), water beetles (such as *Dytiscus marginalis*, *Hydrous piceus*), Gammaridae, *Carabus* spp. and various larvae and small gastropods were also found. Plant matter (grass, piece of rush, seed debris) was found in samples only occasionally and in very small quantities, and was probably consumed with other prey rather than as food itself.

The trophic niche breadth of otters did not differ significantly between the areas (MANOVA, $F_{3,4} = 2.63$, $P = 0.065$), but significant seasonal differences were found ($F_{3,4} = 9.00$, $P < 0.01$), with the widest mean niche breadth in summer ($B = 2.32$) and the lowest in winter ($B = 1.12$). A minimum of 20 different fish, 6 mammal, 6 bird, 3 reptile, 3 amphibian, 12 invertebrate and 3 plant taxa were found in the diet.

**Fish distribution**

The fish consumed by otters were mainly small-sized (Fig. 3) and below 100 g in weight in all areas (biomass estimation; mean: 94.1%; range: 88.0–96.9% between areas). Specimens weighing more than 500 g were rarely taken (0.9–2.1%).
No area-dependent difference was found in the distribution of fish weights among areas (Chi-Square test, $\chi^2_{12} = 20.10$, $P = 0.065$).

The most frequent fish prey were eurytopic species (mean 72.7%, Fig. 3), with stagnophilic species also important (mean 21.7%). Consumption of reophilic species was less important (mean 10.6%).

Table 3. Annual non-fish diet of otters living by streams and channels in the Drava region, Hungary. (*fish and non-fish items together, + = biomass under 0.05%, for abbreviations see Fig. 1 and Table 2).

<table>
<thead>
<tr>
<th>Food taxon</th>
<th>W1</th>
<th>W2</th>
<th>W3</th>
<th>W4</th>
<th>W5</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N%B</td>
<td>N%B</td>
<td>N%B</td>
<td>N%B</td>
<td>N%B</td>
</tr>
<tr>
<td>Mammals</td>
<td>23</td>
<td>9.3</td>
<td>29</td>
<td>5.9</td>
<td>13</td>
</tr>
<tr>
<td>Birds</td>
<td>15</td>
<td>4.1</td>
<td>20</td>
<td>1.9</td>
<td>21</td>
</tr>
<tr>
<td>Reptiles</td>
<td>14</td>
<td>2.1</td>
<td>6</td>
<td>0.7</td>
<td>4</td>
</tr>
<tr>
<td>Amphibians</td>
<td>124</td>
<td>48.5</td>
<td>55</td>
<td>6.1</td>
<td>17</td>
</tr>
<tr>
<td>Crayfish</td>
<td>2</td>
<td>0.1</td>
<td>35</td>
<td>1.7</td>
<td></td>
</tr>
<tr>
<td>Water beetles</td>
<td>86</td>
<td>2.7</td>
<td>83</td>
<td>0.4</td>
<td>28</td>
</tr>
<tr>
<td>Other invertebrates</td>
<td>3</td>
<td>+</td>
<td>3</td>
<td>+</td>
<td>8</td>
</tr>
<tr>
<td>Plants</td>
<td>7</td>
<td>+</td>
<td>3</td>
<td>+</td>
<td>1</td>
</tr>
<tr>
<td>Number of spraints</td>
<td>254</td>
<td>970</td>
<td>308</td>
<td>5.08</td>
<td>327</td>
</tr>
<tr>
<td>Number of items*</td>
<td>443</td>
<td>756</td>
<td>561</td>
<td></td>
<td>561</td>
</tr>
</tbody>
</table>

No area-dependent difference was found in the distribution of fish weights among areas (Chi-Square test, $\chi^2_{12} = 20.10$, $P = 0.065$).

The most frequent fish prey were eurytopic species (mean 72.7%, Fig. 3), with stagnophilic species also important (mean 21.7%). Consumption of reophilic species was less important (mean 10.6%).

Fig. 3. Percentage biomass consumption (mean±SE) of fish prey in the diet of otters living by streams and channels, on the basis of fish weight (a) and guild (b). Fish guilds: RE – reophilic or flow preferring, EU – eurytopic or tolerant for rivers and stagnant waters and ST – stagnophilic or stagnant water preferring; logarithmic scale.

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species was lowest (mean 5.6%). The distribution of food categories was sig- 
nificantly different between areas ($\chi^2_8 = 291.30, P < 0.001$) when looking at fish prey 
guild. Reophilic fish were eaten most by otters at W1 (24.1%) and least at W4 
(0.2%), stagnophilic fish were consumed most at W2 (44.9%) and least at W5 (9.7%), 
and eurytopic fish were taken most at W5 (89.4%) and least at W1 (52.6%).

Non-native fish species, such as giebel carp and brown bullhead (mean 
71.0%), were found most often in the diet. Area-dependent differences were found 
in the distribution of non-native and native fish in the diet ($\chi^2_4 = 196.78, P < 0.001$), 
with non-native fish eaten most at W4 (92.7%), and native species at W1 (68.3%).

DISCUSSION

The diet composition of otters living on the streams and channels studied was 
largely similar with otters preying primarily on fish, as in most studies from areas 
with a moderate climate (JEDRZEJEWSKA et al. 2001, CLAVERO et al. 2003). These 
results were also similar to studies of small watercourses in northern latitudes 
(ERLINGE 1967, WEBER 1990, HARNA 1993, SIDOROVICH 1997), where fish, and 
occasionally amphibians, were the main food of otters. The consumption ratio of 
fish as primary food showed a characteristic seasonal pattern with an increasing 
trend from spring to winter, although differences were found between areas. The 
seasonal changes may be caused by fluctuation in the fish availability, which is in-
fluenced by the water discharge conditions. A short period or drying, of changing 
from flowing to stagnant water occurred on the studied small channels (W1, W2 
and W5) or stream (W4) especially during the late summer/early autumn period, 
which may have a considerable effect on the density and composition of the avail-
able fish (and other aquatic) communities.

On the small watercourses in this study, highest supplementary food con-
sumption was found in spring (e.g. amphibians) and, in some areas, theses items 
(such as small mammals, birds, reptiles and invertebrates) continued to be impor-
tant during summer. In the main otter habitats in other European regions, such as 
ponds and rivers (e.g. KRAZ 2000, JEDRZEJEWSKA et al. 2001, COPP & ROCHE 
2003, LANSZKI & MOLNÁR 2003, REMONTI et al. 2008), supplementary foods are 
mainly important in winter and spring, usually in relation to fluctuations in fish 
supply. Higher spring and summer consumption of supplementary foods may also 
be in relation to changes in the relative abundance of possible prey, i.e. early spring 
is the spawning period of amphibians, or spring and summer is the nesting period 
of birds, consequently they become easier to catch. In this study amphibians were 
the most important supplementary food of otters (Fig. 2. and Table 2). Moreover,
in one location (W1) amphibians were primary foods, except in winter. Amphibians might be seasonally accessible not only in the bed of the channel, but on the adjacent habitats such as wet grasslands and small forest patches. High consumption ratios of supplementary foods were found for otters living along small watercourses both in northern and southern latitudes. Weber (1990) noted higher amphibian consumption in late winter and spring, Harna (1993) higher amphibian consumption in spring, and Gourvelou et al. (2000) higher bird consumption in autumn and higher mammal and amphibian consumption in winter. The consumption ratio of invertebrates in this study was lower than in Sweden (Erlinge 1967) or in the Mediterranean region (Beja 1996, Gourvelou et al. 2000) where, besides the dominant fish, crayfish was a seasonally important secondary food item of otters living in streams or channels. In the present study, consumption of the native crayfish (Astacus astacus) was found to comparatively high only in one location (W3), especially in summer, and occurred occasionally only in another location (W2). (W3 is the largest studied watercourse with the most balanced discharge.)

The importance of crayfish, as the introduced American crayfish (Procambarus clarkii) in the diet of otters in Mediterranean areas is high, both in lotic and lentic systems, as was found in several studies (e.g. Beja 1996, Magalhães et al. 2002, Clavero et al. 2003, 2004, Ottino & Giller 2004, Pedroso et al. 2006).

Otter reproduction does not show strict seasonality in the Pannonian region, as in most European biogeographic regions (Lanszki et al. 2008b) and, what is more, summer droughts or low discharge (such as that experienced on the streams and channels in this study, e.g. at W1, W4 and W5) may be disadvantageous to reproduction success (Ruiz-Olmo et al. 2002) as they provide sub-optimal conditions for otters due to lowered food availability. Under such conditions, otters may have to increase their home range size (Erlinge 1968). Numerous studies and overviews (e.g. Erlinge 1968, Jefferies 1986, Kruuk et al. 1986, Mason & Macdonald 1986, Kruuk 1995, Carss 1995) detailed that sprainting behaviour and therefore the number of seasonal spraints collected is influenced by numerous factors, e.g. season, water temperature, fish biomass. The occurrence of otters along the watercourses in this study, however, appeared to remain more or less constant, despite lowered spraint sample sizes (Fig. 2). This is presumably due to local, short-term, unfavourable environmental conditions (Lanszki & Sallai 2006), and to rapid spontaneous restocking with fish as the water level rises across the network of watercourses (Fig. 1). Sub-optimal conditions were indicated by a high number of other food taxa (33) beside the 20 fish taxa in the diet. Although otters are able to prey on a range of species (Chanin 1985, Mason & Macdonald 1986, Kruuk 1995), including invertebrates, amphibians and birds (Erlinge 1967, 1968).
KRUUK 1995, JEDRZEJEWSKA et al. 2001, RUIZ-OLMO et al. 2001, CLAVERO et al. 2003, 2005), in optimal conditions the main food remains fish. Reophilic fish consumption was low. A survey of fish at the study sites was not undertaken and, therefore, actual fish availability is unknown, but it can be assumed from fish surveys performed in small watercourses of the Drava region (SALLAI 2002, Z. SALLAI pers. comm.). Fish surveys (SALLAI 2002a,b, and Z. SALLAI pers comm.) performed during spring and summer of 2000 on small watercourses of the Drava region (especially for the W3 location) provide information about the character of the fish resource in small watercourses. The lack of larger sized fish taken by otters may depended on their rarity in the watercourses. The characteristic two species of these watercourses were the native eurytopic roach (mean: 45.5%, range: 5.0–62.2%) and also eurytopic bleak (mean: 32.4%, range: 20.7–36.8%), but there were also the eurytopic giebel carp (mean: 6.5%) and stagnophilic stone morroco (mean: 4.8%). Previous studies, however, indicate a relationship between fish availability and the composition or preference for fish species in the diet of otters (ERLINGE 1967, KRUUK 1995). At the same time, preference for the roach and the very small sized stone morocco in fish pond and stream areas (LANSZKI et al. 2001), and also in the Drava River (LANSZKI & SALLAI 2006) were positive but relatively low (Ivlev’s preference index, Ei: 0.39 for roach and 0.28 for bleak in fishponds and streams, and Ei: 0.04 and 0.16, respectively on the Drava River). Furthermore preference of these fish species largely fluctuated depending on the composition of the fish availability. In our study areas the consumption of common, small-sized and generally non-native eurytopic species (such as giebel carp, brown bullhead) was predominant. As these species were relatively rare in the small watercourses, it seems that otters preferred explicitly these, and the same was found in ponds and the Drava River (LANSZKI et al. 2001, LANSZKI & SALLAI 2006). While in the food sources the native fish species dominated (appr. 80–90% of fish in the small watercourses, SALLAI 2002a,b and Z. SALLAI pers comm.), the main food of otters generally consisted of non-native fish species (e.g. 67% on W3).

In conclusion, otters living on small watercourses with a low discharge took fish as their principle food and amphibians as secondary food taxa. Fish food mainly consisted of small-sized and common eurytopic non-native fish. Due to the ecological adaptability of otters, they can survive short-term sub-optimal periods by shifting dietary preference to supplementary food species, such as amphibians, birds, crustaceans or mammals, until fish availability increases once again. It is not known, however, whether such conditions impose long-term effects on the reproduction ability/success or physical fitness of otters. The results show that small watercourses also play an important role in the ecological network as regards otter...
habitat (at least as feeding places) and, as such, indicate that the whole water-course, from source to sea, should be addressed when either monitoring or managing otter habitats.

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