CAPTURE AND CONSUMPTION OF PREY OF THE OTTER (Lutra lutra) IN MEDITERRANEAN FRESHWATER HABITATS OF THE IBERIAN PENINSULA

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ABSTRACT

The otter feeds almost exclusively on aquatic and semiaquatic species, catching them in watercourses and waterbodies. Foraging and prey consumption studies in freshwater habitats are scarce. Iberian otters caught between 3 and 5 fish/hour of observation in Mediterranean rivers, except during periods of fish shortage, when dropped to 1 fish/hour or less. On 98.2% of occasions the consumption of prey took place in the water, upon river features such as rocks, islands or stones, or at less than 1.50 m from the water edge. Almost all fish of less than 100 g were eaten whole, but left parts of large fish; gravide fish females; claws, legs and heads of crayfish; and toad skins. A food-limited species like the otter is under pressure to optimise the use if its food resources. The prey or parts of prey are left as a last resort in order to avoid injury, intoxications, because the daily food needs have been met, because disturbance, or because of immature behaviour in the case of cubs. For this reason, densities of fish remains are very low, but crayfish and toad remains densities can be high. Density of remains of prey depends more on the characteristics of the prey than the abundance of otters and prey. Results obtained are of importance when evaluating the biomass of the prey in the studies of diet, because parts of prey which are not consumed systematically.

Key words: Food, Mediterranean habitats, Otter, predation.

RESUMEN

Captura y consumo de las presas por la nutria (Lutra lutra) en hábitats fluviales mediterráneos de la Península Ibérica

La nutria se alimenta casi exclusivamente de especies acuáticas y semiacuáticas, que captura en de cursos y masas de agua. Los estudios sobre la búsqueda, captura y consumo de las presas son escasos. Los ejemplares ibéricos capturaron entre 3 y 4 peces/hora de observación en ríos mediterráneos, excepto durante épocas de escasez de peces, descendiendo entonces a 1 pez/hora o menos. En un 98.2% de las ocasiones, las presas fueron consumidas en el agua, en una roca, piedra, isla o similar, o a menos de 1,50 m de la orilla. La práctica totalidad de los peces de menos de 100 g fueron consumidos por entero, pero abandonaron partes significativas de los peces mayores, de las hembras grávidas de peces, de cangrejos (pinzas, patas y cabezas) y de pieles de sapos. Una especie limitada por la disponibilidad de alimento, como es el caso de la nutria, está bajo presión para optimizar el uso de sus recursos. Las partes de las presas abandonadas son una forma de evitar heridas o intoxicaciones, aunque pueden serlo por también saciedad, molestias o por la conducta de juego de las crías. Por estas razones, las densidades de restos de presas son muy bajas, excepto local o temporalmente para cangrejos o sapos. La densidad de restos depende más de sus características que de la abundancia en el medio de nutrias y de presas. Los resultados obtenidos son de importancia para la evaluación de la biomasa ingerida de cada categoría de
presas en los estudios sobre la dieta, ya que algunas partes de las presas son abandonadas sistemáticamente.

Palabras clave: Alimentación, depredación, hábitats mediterráneos, Nutria.

**INTRODUCTION**

The otter population has declined dramatically in Europe during the 20th century, due mainly to the transformation of its habitat as a consequence of human activity (Mason and MacDonald 1986). In the Iberian Peninsula, the first studies which demonstrated this decrease were published during the 1970's and the beginning of the 1980's (Blas-Aritio 1970, 1979; Ferrand de Almeida 1980; Delibes and Callejo 1985).

Studies on otter diet have proliferated during the last two decades (Mason and MacDonald 1986; Kruuk 1995; Ruiz-Olmo and Palazón 1997). These compilations have enabled us to establish which species they consume in various environments and how they vary over time. The otter feeds almost exclusively on aquatic and semiaquatic species (Ruiz-Olmo 1995a), catching them near watercourses and waterbodies. Besides factors such as pollution and the transformation of its habitat, food availability also plays a key role in its conservation, regulating the parameters related to breeding, mortality, abundance and finally, distribution: the otter is food limited (Kruuk 1995; Carss and Kruuk 1996; Ruiz-Olmo 1998; Ruiz-Olmo et al. in press). Due to the thermoregulation needs of an animal which does not have a thick layer of insulation, and which lives in an aquatic environment in which the temperature is generally lower than that of the body (Kruuk 1995; Kruuk et al. 1997), as in the case of the otter, food needs are of even greater importance especially because their energetic needs are approximately 20% greater than those expected for their size (McNab 1989).

However, despite the importance of its alimentary ecology, little is known about its predation behaviour, foraging and energetic balance. Those aspects would enable us to acquire a deeper understanding when interpreting its ecology and establishing more consistent management measures. The otter is not found in great abundance within its habitats, living in low densities. Furthermore, to date, it has been considered as a mainly nocturnal species of shy habits, thus making its study notably difficult, unlike marine environments in the North of Europe, where otters are largely diurnal (Kruuk 1995).

Moreover, recent studies criticising the way in which most research on the otter diet is based on traditional methods of spraint analysis have been carried out (Ferrario et al. 1995; Jacobsen and Hansen 1996; Carss and Elston 1996; Carss and Parkinsson 1996; Knollseisen and Kranz 1998). To summarise, spraints do not
constitute independent samples, since the remains of a prey item can appear in more than one excrement and larger prey tend to be overestimated (with remains being distributed in more excrements), as with prey which have a greater proportion of hard parts. Those authors conclude that in order to fully understand the diet, individual pieces which only appear once in the skeleton should be used (for example, the atlas vertebrate in the Salmonidae family), and the rest discarded. Despite constituting a notable advance in the precision of studies on otter diet, they do not tackle one important aspect: whether the finding of one particular bone means that the whole prey has been consumed? The answer to this question is basic when reliably establishing the biomass of the distinct categories of prey in diet (both species and size) to determine the energetic balance of the otter.

While these studies are scarce in Europe as a whole, in Mediterranean countries they are practically non-existent, and the only data on this subject was presented in Ruiz-Olmo (1995 b). The present study elaborates on this knowledge and provides information on a practically unknow field of the Eurasian otter.

**Study area**

The current study was carried out in several rivers situated in the NE Iberian Peninsula (Catalonia, Community of Valencia, and Aragón). Transects were carried out in each area in the search for otters in the basins of the rivers Cinca, Isábena, Ésera, Noguera Ribagorçana, Noguera Pallaresa, Segre, Montsant, Guadalope, Bergantes, Matarranya, Algars, Muga and Fluvià. For a description of the physical geography, the characteristics of the rivers and the human geography, the works of Riba et al. (1979), Folch et al. (1986), Santanach et al. (1986) and Terrades et al. (1989) can be consulted. These studies focused on Mediterranean and Pyrenean rivers, which are all greatly conditioned by rainfall - the former, fundamentally pluvial and the latter, pluvio-nival-. All the rivers studied have a minimum flow in summer, and a maximum flow in spring and autumn. With the exception of the rivers Bergantes, Matarranya and Algars, there are dams of several types and sizes, which modify and regulate the regime of the river.

The dominant species in the studied rivers of the Ebro Basin which form the basis of the otter diet are barbels (Barbus graellsi and B. haasi), French nase (Chondrostoma toxostoma) and more recently, the American crayfish (Procambarus clarkii), although in areas of altitude these are substituted by trout (Salmo trutta) and, in spring by amphibians (Bufo bufo, Rana perezi and R. temporaria) (Ruiz-Olmo and Palazón 1997). Other species which are locally basic in diet are (or were until recently) the viperine snake (Natrix maura), the chub (Leuciscus cephalus), the
Iberian roach (Rutilus arcasii), the carp (Cyprinus carpio), the gudgeon (Gobio gobio), the bleak (Alburnus alburnus), the black-bass (Micropterus salmoides), the rainbow trout (Onchorhyncus mykiss), the European crayfish (Austropotamobius pallipes) and several species of aquatic insects.

In the basins of the rivers Fluvià and Muga, the main species are the American cray fish, the eel (Anguilla anguilla), the Catalan barbel (Barbus meridionalis), the Iberian roach (Rutilus lemmingi), the carp, the chub, some other euryhaline fish species (Chelon sp., Liza sp., Dicentrarchus labrax), amphibians, water snakes and insects (own unpublished observations).

It should be pointed out that in the two main transect surveyed monthly during the transects surveyed monthly for the detection of otter prey remains (both in the Ebro basin), the following conditions were present (Ruiz-Olmo 1995 b and our unpublished data):
- The river Noguera Pallaresa. Is a mountain stretch with 0.05-0.10 otters.km^{-1} and an average value of 9 g.m^{-2} of fish (standard length greater than 5 cm). It was chosen because the otter feeds almost exclusively on medium and large-sized trout (S. trutta).
- The river Noguera Ribagorçana. Is a medium mountain stretch with 0.70-0.90 otters.km^{-1} and 46.5 g.m^{-2} of fish (basically B. graelisi and Ch. toxostoma), during the study. A wild otter female was radiotracked in November 1992.

In the river Bergantes (where the radiotracking of tagged otters was carried out between 1997 and 1998), also in the Ebro basin, the estimated otter density ranged between 0.2 and 0.4 otters.km^{-1}, and the availability of fish was between 2.0 and 25.2 g.m^{-2}, almost exclusively B. graelisi and Ch. toxostoma (our unpublished data).

**Material and methods**

Systemised transects

Between 1984 and 1998, numerous systemised surveys were carried out in the rivers of the study area in which otters were present. Many took place during the otter surveys of 1984-85, 1989-90 and 1994-1996 (Ruiz-Olmo 1995 a; Ruiz-Olmo and Delibes 1999). These consisted of the search for otter signs (excrements and tracks) in the watercourses and waterbodies, according to the standard methodology of sites 600 m long (Mason and MacDonald 1986; Delibes 1990). These surveys were complemented with others which were carried out during several studies: the collection of excrements for studies on diet, track censuses, the study of dens, etc. In this way, 311 km of river were covered throughout this period.
Moreover, two stretches from the rivers Noguera Ribagorçana (2.0 km) and Noguera Pallaresa (2.6 km) were selected and were surveyed monthly between November 1989 and October 1990. In total, 24.0 and 31.2 km were covered respectively, throughout the 12 month study.

Most sample strips included a band 5 m wide from the water edge on each of the riverbanks.

During all surveys, special attention was paid to the detection of all otter prey and remains. Given that in the study area there are many species of mammals, birds and even reptiles which feed on fish, amphibians, snakes and crayfish (constituting more than 99 % of the otter diet in the study area in most of the locations; Ruiz-Olmo and Palazón 1997), a special emphasis was placed on rejecting all prey when there was reasonable doubt as to the predator species. Only remains that could be attributed exclusively to the otter were considered and collected, the rest were rejected. Only those cases in which otter excrements or footprints were found together with the prey or near the prey were considered.

Direct observation of otters

Information was also obtained from the radiotracking of four wild otters which displayed diurnal activity during the autumn and winter, and which were followed at a distance without disturbing using 10 x 40 binoculars. An adult female weighing 4.8 kg with a subcutaneous implantation was tracked for 20 days in the river Noguera Ribagorçana in November 1992. In addition, three individuals in the river Bergantes were tagged with an intraperitoneal implant: one male weighing 7.0 kg was tracked for 111 days, one female weighing 4.4 kg was tracked for 254 days and another male weighing 7.8 kg was tracked for 117 days (the observations were carried out during the winter of 1996-97).

In all four cases the total length of observation time was taken into account (start and finish time), along with the total number of prey caught and consumed, the time invested in its consumption (until it was finished or left, even if this implied a change of position), except for the river Bergantes, the place where the prey was consumed and, where possible, the species and size of the prey. Special care was taken to observe where it was consumed, to visit the exact place later (measuring the distance to the water edge and above the water level) and to collect the remains.

Moreover, between 1984 and 1999 systematic otter censuses were carried out during the crepuscular periods (nightfall and daybreak), on the riverbanks set aside for otter observation in three Pre-Pyrenean rivers (Noguera Ribagorçana, Noguera Pallaresa and the Segre). These censuses involved experienced observers. In addition, other non-systemised vigils were carried out exclusively by the authors of the present
study. 1,780 individual vigils were carried out, which covered a total of 3,033 h. The same methodology was applied to each otter observed as in the case of the radiotracked otters.

In the present study, a pool of prey is considered to be all those prey items which are found at less than a metre from each other.

Studies on otters in captivity

Finally, the field studies were complemented with observations of four otters in captivity (Table 1):

- Wildlife Recovery Centre of “El Saler” (Valencia). An alimentary test was carried out on two males weighing 6.1 kg and 5.5 kg. The animals remained in enclosures measuring 19 m$^2$ in which there were small pools of water. They were given 505 fish between January and April in 1991. Only 379 were eaten by otters; the species offered are presented in Table 1.

- Otter Centre, El Pont de Suert (Lleida). During August and September 1997, a total of 138 live fish were offered to two otters (siblings), a male weighing 8 kg and a female of 6 kg, which were approximately one and a half years old. Both were kept in an enclosure measuring 106 m$^2$, of which half was water (approximately 1 m deep).

In both cases, a variety of fish species and sizes were given to the otters, which fully satisfied their needs. All the fish were weighed and measured. In “El Saler”, it was only established if the fish had been totally or partially consumed, or left untouched. In El Pont de Suert, all the remains were collected and later weighed.

<table>
<thead>
<tr>
<th>Fish offered to the otters in the study</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Table 1</strong></td>
</tr>
<tr>
<td>Fish offered to the otters in captivity</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Fish</th>
<th>El Saler</th>
<th>El Pont de Suert</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>&lt;100 g</td>
<td>100-300 g</td>
</tr>
<tr>
<td><em>Salmo trutta</em></td>
<td></td>
<td>-</td>
</tr>
<tr>
<td><em>Anguilla anguilla</em></td>
<td>38</td>
<td>10</td>
</tr>
<tr>
<td><em>Micropterus salmoides</em></td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Barbus guiraonis</em></td>
<td>51</td>
<td>91</td>
</tr>
<tr>
<td><em>Barbus graellsi</em></td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Chondrostoma toxostoma</em></td>
<td>12</td>
<td>-</td>
</tr>
<tr>
<td><em>Carassius auratus</em></td>
<td>64</td>
<td>66</td>
</tr>
<tr>
<td><em>Cyprinus carpio</em></td>
<td>73</td>
<td>21</td>
</tr>
<tr>
<td><em>Mugil cephalus</em></td>
<td>-</td>
<td>6</td>
</tr>
</tbody>
</table>
RESULTS

Capture of Prey

During the vigils, 216 otter observations were made, to which another 75 observations of otters tagged with transmitters were added (291 observations of otters). In total, they were observed for more than 19 hours, during which they caught 62 fish and a viperine snake (N. maura); all the individuals foraged and displayed activity always in the water or in the riverbanks, generally at less than 5 m from the water edge.

In most of cases, the otters caught between 3.0 and 4.9 fish/hour of observation (Table 2): 14 B. graellsi, 24 Ch. toxostoma and 1 S. trutta; on 23 occasions the species could not be identified. In all the cases in which the total length could be established, most of the fish were between 10 and 20 cm long (77%; n=47). During a period of great food scarcity, the capture rate dropped to 0.96 fish/hour. It should be pointed out that all the prey were caught by adults or subadults, and only once was a young otter, accompanied by its mother, observed catching a fish. The young otter was the same size as its mother, and she had refused to share a previous catch.

TABLE 2
Fish capture rate for the otters tracked at a distance with the help of binoculars
Tasa de captura de peces por las nutrias seguidas a distancia mediante prismáticos

<table>
<thead>
<tr>
<th>Site</th>
<th>Method</th>
<th>Season</th>
<th>Total time of observation</th>
<th>Rate (Fish/hour)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prepyrinean</td>
<td>Visual censuses</td>
<td>Summer (1990-1992)</td>
<td>8 h 19 min</td>
<td>3.37</td>
</tr>
<tr>
<td>Prepyrinean</td>
<td>Radio-tracking (1 female)</td>
<td>Autumn 1992</td>
<td>3 h 08 min</td>
<td>0.96</td>
</tr>
<tr>
<td>Prepyrinean</td>
<td>Visual censuses</td>
<td>Summer 1993 - 1999</td>
<td>3 h 38 min</td>
<td>3.03</td>
</tr>
<tr>
<td>Bergantes river</td>
<td>Radio-tracking (3 otters)</td>
<td>Autumn-Winter 1996 - 97</td>
<td>3 h 39 min</td>
<td>4.93</td>
</tr>
<tr>
<td>TOTAL</td>
<td></td>
<td></td>
<td>19 h 44 min</td>
<td>3.14</td>
</tr>
</tbody>
</table>

Consumption of prey

The visual tracking of wild otters demonstrated that 85.7% of prey-items of less than 10 cm (n=8) were consumed immediately in the water. Of the remaining 54 prey items, on 9% of occasions the otter left the field of vision once the prey was caught, but the rest of the time it made its way to a nearby, fixed point (a stone, a rock, gravel, earth), without hiding; only three otters partially hid amongst the helofitic vegetation (Typha and Enea spp.), but leaving the lower half of the body sticking out. On 98.2% of occasions (n=57) the consumption of prey took place in the water, upon river features such as rocks, islands or stones, or at less than 1.50 m from the water edge; thus most of the prey remains were found in a narrow strip adjacent to both banks and on the features found in the river.
The average time taken to consume the prey by wild otters was 1.54 minutes (S.D.=1.45 minutes; n=45). Most prey were consumed in less than a minute (62.2%; n=45), and 88.9% in less than 5 minutes. A significant correlation was found (r=0.97; p<0.0001) between the size of the fish and the time invested in its consumption (Fig. 1), which oscillated between 8.25 seconds (S.D.=14.5 seconds; n=4) with those measuring less than 10 cm, and more than 10 minutes for the only one caught measuring 30-35 cm. The relationship is expressed as follows (time in minutes; length in cm):

\[
\text{Time of consumption} = -4.02 + 0.40 \text{total length}
\]

Table 3 shows the data corresponding to the way in which the 63 fish caught by captive otters (those where it was possible to check where the otter began its consumption) were eaten. Otters preferred to start with the head (87.2% of barbels and trout together; n=47), whilst eels were consumed indistinctly beginning with the head or the tail. The barbels and trout that were eaten tail-first were generally large.
Capture and consumption of prey by otters

Table 3
Percentage of times in which the consumption of fish offered to the otters in captivity in El Pont de Suert began with the head or tail

<table>
<thead>
<tr>
<th></th>
<th>Head</th>
<th>Tail</th>
<th>n</th>
<th>significance (1)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anguilla anguilla</td>
<td>44.75</td>
<td>56.25</td>
<td>16</td>
<td>0.723</td>
</tr>
<tr>
<td>Salmo trutta</td>
<td>84.6</td>
<td>15.4</td>
<td>26</td>
<td>0.008</td>
</tr>
<tr>
<td>Barbus graellsi</td>
<td>90.5</td>
<td>9.5</td>
<td>21</td>
<td>0.011</td>
</tr>
<tr>
<td>TOTAL</td>
<td>76.2</td>
<td>2.8</td>
<td>63</td>
<td>0.004</td>
</tr>
</tbody>
</table>

(1) Chi-square test

In figure 2 it can be observed that as the weight of the prey increases, so does the probability that it is only partially eaten. Almost all fish of less than 100 g were eaten whole (99.6% of the 240 fish given to the four otters in captivity weighing less than 100 g), whilst the otters left parts of the majority of prey weighing over 700 g (only 36.7% of the 11 fish over this weight were completely eaten). Fish of less than 300 g were completely consumed (not considering scales and other small remains left over accidentally) in 87.7% of the cases (n=407).

Figure 2. Percentage of fish which the captive otters left uneaten (remains) in relation to the biomass of the fish. In the case of Pont de Suert the remains exceeding 10 g are differentiated from those which exceeded 50 g

Porcentaje de los peces en relación a su biomasa, que las nutrias mantenidas en cautividad no ingerían. En el caso del Port de Suert, se muestran los restos que sobrepasaron los 10 g y 50 g
A significant correlation was found between the weight of the fish consumed and the percentage of fish that were not consumed by otters:

(a) considering all the fish consumed \( (r=0.58; p<0.001) \) and,
(b) considering only those that were not eaten whole \( (r=0.565; p=0.001) \).

Remains of prey

During the field studies, it was confirmed that the remains of the otter prey were not easily found, except in the case of the American crayfish which are abundant \( (1.0-9.32 \text{ remains/km}) \) and amphibians in environments where they group together in order to reproduce or move \( (4.2 \text{ remains/km}) \)(Table 4). In places where the otter feed almost exclusively on fish, remains are scarce \( (0-0.5 \text{ per km}) \).

<table>
<thead>
<tr>
<th>Basin</th>
<th>River or site</th>
<th>Dominant species in diet</th>
<th>Km covered</th>
<th>Remains of prey</th>
<th>Remains/km</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ebro</td>
<td>Nog. Pallaresa (*)</td>
<td>Trout - Cyprinids</td>
<td>112.8</td>
<td>10</td>
<td>0.09</td>
</tr>
<tr>
<td></td>
<td>Esera</td>
<td>Trout</td>
<td>15.5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Nog. Ribagorçana medio (+) (+)</td>
<td>Barbels and French nase</td>
<td>31.9</td>
<td>7</td>
<td>0.22</td>
</tr>
<tr>
<td></td>
<td>Isàbena (+)</td>
<td>Barbels and French nase</td>
<td>8.2</td>
<td>4</td>
<td>0.5</td>
</tr>
<tr>
<td></td>
<td>Segre</td>
<td>Trout and Cyprinids</td>
<td>11.1</td>
<td>2</td>
<td>0.18</td>
</tr>
<tr>
<td></td>
<td>Cinca (Until 1992)</td>
<td>Cyprinids</td>
<td>6.7</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Cinca (1993-1998)</td>
<td>American crayfish and/or Cyprinids</td>
<td>20.5</td>
<td>191</td>
<td>9.32</td>
</tr>
<tr>
<td></td>
<td>Montsant</td>
<td>Barbs, French nase and indigenous crayfish</td>
<td>15.9</td>
<td>5</td>
<td>0.31</td>
</tr>
<tr>
<td></td>
<td>Guadalope</td>
<td>American crayfish, barbels and French nase</td>
<td>3.1</td>
<td>6</td>
<td>1.94</td>
</tr>
<tr>
<td></td>
<td>Bergantes</td>
<td>Barbs and French nase</td>
<td>10</td>
<td>1</td>
<td>0.10</td>
</tr>
<tr>
<td></td>
<td>Matarranya (+)</td>
<td>Barbels and French nase</td>
<td>29.8</td>
<td>9</td>
<td>0.30</td>
</tr>
<tr>
<td></td>
<td>Algars (until 1992) (+)</td>
<td>Barbels and French nase</td>
<td>10.7</td>
<td>2</td>
<td>0.19</td>
</tr>
<tr>
<td></td>
<td>Algars (1993-1998)</td>
<td>Barbels, French nase and American crayfish</td>
<td>3.7</td>
<td>4</td>
<td>1.08</td>
</tr>
<tr>
<td></td>
<td>Mountain lakes (&gt;-1500 m)</td>
<td>Amphibians and trout</td>
<td>4.2</td>
<td>30</td>
<td>7.14</td>
</tr>
<tr>
<td></td>
<td>Alguamolls de l’Empordà</td>
<td>Fish and American crayfish</td>
<td>11.6</td>
<td>8</td>
<td>0.69</td>
</tr>
<tr>
<td></td>
<td>Muga</td>
<td>American crayfish and/or fish</td>
<td>5.8</td>
<td>26</td>
<td>4.51</td>
</tr>
<tr>
<td></td>
<td>Fluvia</td>
<td>Fish</td>
<td>9.6</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

(*) Does not include the transects carried out in the structures of 2.0 and 2.6 km surveyed monthly.
(+ ) Includes at least one otter female with youngs.

In the stretch of the river Noguera Pallaresa which was checked monthly and where there are abundant populations of medium and large-sized trout, a total of
Capture and consumption of prey by otters

0.51 remains/km were found and in the river Noguera Ribagorçana (almost exclusively barbels and French nase), 0.08 remains/km were found. The differences were significant ($X^2=6.21$, df=1, $p=0.013$).

Given that significant differences were not found between the distances to the riverbank between fish, crayfish and amphibians, the total distance of remains from the water edge was established (Fig. 3). 31.1% of the prey remains were found in the water and 58.9% on land at less than 1.5 m from the riverbank; the most distant remains were found at 5.5 m. Amphibians remains were found more often in the water (76.2% of prey remains, n =21) than fish (11.5%, n=80) and crayfish (14.1%, n=156). The crayfish were found furthest away from the river.

Similar results were found with the position of prey remains above water level (Fig.4). Only 2.7% of prey remains were found at more than 1 m above this, with a maximum of 1.95 m.

Of 230 pools of prey remains, only 8.3% contained more than one prey item, with maximum accumulations of 5 and 6 crayfish. 73.7% of the pools with more than one prey remain (n=19) were found to be associated with the presence of cubs (observed directly or detected by their tracks), while on two occasions (11.8%) the tail-end remains of four gravid female fish and on another two occasions, toad remains (Bufo bufo), with the skins turned inside out were found. Regarding American crayfish remains, claws were the most frequently left part (94.5%, n=163), followed by the legs (57.1%), the head (35.6%) and the tail (3.1%) ($X^2=292.35$; d.f=3; $p<0.0001$). With fish, (omitting those found almost whole, sometimes left because of some disturbance, and without taking into account scales which are lost accidentally), the head or fragments of it (mainly phaeringeal teeth, jaws or other large bones) have rose the maximum values with 27.8% (n=72), the pectoral fin 12.5%, the intermediate part of the body 11.1% and the tail 9.7% ($X^2=11.80$; d.f=3; $p=0.008$). Finally, of the 21 amphibians found (all of which Bufo bufo) the otters left the skins turned inside out including the parotid glands and the head, except in one case which only included the back legs.

**Discussion**

Consumption of prey

Our results suggest that the otter tends to exploits its preys to the full. Otters consume the smallest fish (corresponding approximately to those measuring less than 25 cm or less than 150 g) whole, data which coincides with that of Erlinge (1967, 1968), Chanin (1985) and Kruuk (1995). If we take into account that the otter tends to eat small fish, with an average weight of 17-72 g in the centre and north of Europe
(Jenkins and Harper 1980; Wise et al. 1981; Kyne et al. 1989; Watt 1991; Brzezinski et al. 1993; Kruuk 1995; Carss and Kruuk 1996) and 30-82 g in the Iberian Peninsula (Callejo 1984, 1988; Ruiz-Olmo 1995a; Bartolomé et al. 1997), we will see that a significant number of the fish caught are eaten whole. In our study area, 80-90% of fish caught did not exceed 150 g (Ruiz-Olmo 1995a; Bartolomé et al. 1997).

Contrarily, almost all of the American crayfish consumed weigh less than 40 g (Beja 1995), but in this case, some parts were systematically left.

Six times more fish remains were found in the river Noguera Pallaresa, when the estimated density of otters was seven or eight times lower and the biomass of fish some five times lower than in the river Noguera Ribagorçana. In the last river, the fish consumed by the otter weighed on average 81 g, whilst in the Noguera Pallaresa they reached 182 g (Ruiz-Olmo 1995a). In the river Noguera Pallaresa, the
that were left were always jaws and head bones of large trout, generally measuring 30 cm or more (in all cases, over 20 cm). Thus density of remains depends more on the characteristics of the prey than the abundance of otters and prey.

Figure 4. Distance above the water level in which the wild otters consumed their prey (amphibians, fish, american crayfish and as a whole) in the north-east of the Iberian Peninsula (data in percentages)

Altura sobre el nivel del agua a la que las nutrias consumieron sus presas (anfibios, peces, cangrejo rojo americano y en su conjunto) en el noreste de la Península Ibérica (datos en porcentajes)

The prey, or parts of it, that are partially consumed and remains are left usually correspond to large fish (on some occasions we confirmed that these were sick or wounded fish, or fish which were exhausted by the effort involved in reproduction as was demonstrated in salmon; Carss et al. 1990), parts which are difficult to digest or which can damage the digestive tract (pharingeal teeth, jaws or bones from large fish, or crayfish claws and legs), parts containing eggs or unpleasant tasting or toxic glands (outputs of fish eggs, external fungal infestations, amphibian parotid glands and skins), or parts accidentally lost during consumption or prey left by cubs (through learning behaviour and playing) (Erlinge 1968; Watson 1978; Fairley 1984;

A food-limited species like the otter (Kruuk and Carss 1996), with a high basal metabolism (McNaab 1989), making it significantly vulnerable to low temperatures and fluctuations in food availability (Kruuk et al. 1994) and with a low digestibility of its prey (Kruuk and Carss 1996) is under pressure to optimise the use if its food resources. This also explains why the densities of fish remains were so low in our study area (see also Mason and MacDonald 1986). The prey or parts of prey are left as a last resort in order to avoid injury, intoxications, because the daily food needs have been met, or because of immature behaviour in the case of cubs.

Small prey are consumed immediately in the water, behaviour which coincides with the results from studies on coastal otters in the north of the British Isles (Kruuk et al. 1990; Kruuk 1995) and in captivity (Erlinge 1968). But most medium or large prey are carried to a nearby point on the bank, an island, a stone or a rock where the otter can eat it, generally within a few minutes. The otter consumes its prey openly. Kruuk (1995) indicates that in marine environments, otters carry the larger or most difficult prey to the shore; invariably, crabs are consumed on the shore (leaving the claws, legs and exoskeleton) and so too are P.clarkii if we note the high density of remains found in some areas (see also Watson 1978). The need to work on this prey in order to extract claws could justify this.

Regarding the way otters begin to consume fish, the head seems to be the most habitual starting point. This was pointed out by Erlinge (1968) and could be due to the necessity to kill prey as quickly as possible to avoid injuries. However, with large fish this priority does not seem to occur and it is not infrequent for the otter to begin with the tail or the side; in these cases, the fact that the otter frequently leaves the heads or parts of the heads could have an influence. Carss et al. (1990) show that otters partially consume large salmon (an average weight of 2.9 kg), mainly eating the side. Erlinge (1968), coinciding with our findings also points out that otters prefer to consume the tail and thorax of crayfish first.

Studies on otter diet

Moreover, the results obtained are of importance when evaluating the biomass of the prey in the studies of diet. Recently, several authors have revised the conventional methods of collecting and analysing spraints, and have criticised the way in which the size and biomass of prey (mainly fish) are estimated, based on the presence of determined non-singular pieces of bone which have varying probabilities of being detected in samples (Ferrario et al. 1995; Jacobsen and Hansen 1996; Carss and Elston 1996; Carss and Parkinsson 1996; Knollseisen and Kranz 1998). These studies
contribute to improved precision in the study of otter diet. Our results indicate that those studies should be questioned even further if we consider that parts of prey which are not consumed. In some cases, they are systematically left by the otter (for example, the American crayfish claws, toad skins or the end part of the tail of small gravid female French nases) but in others they are left because they are large fish of which the otter only eats a small part (see also Carss et al. 1990). The number of fish caught can be estimated correctly but the food or energy contribution of large fish, crayfish or gravid female fish, for example, can be overestimated. In a diet study, the total biomass of a prey is often calculated from the presence of a piece of bone. But this is not strictly true, because the majority of large fish are only partially eaten. Thus, in addition to the factors of correction which have been applied to the prey digestibility (Ferrario et al. 1995; Carss and Elston 1996) or the factors of correction corresponding to the energetic or calorific value (Beja 1995; Kruuk and Carss, 1996), other factors of correction related to the proportion of biomass not consumed should be added. Biomass of parts left uneaten can be different at some point in the year.

Otter’s food needs

The otter’s food needs have been fixed at 12-15% of its corporal biomass (Kruuk et al. 1993). This percentage can have several interpretations if we consider the partial consumption of prey. Based on this assumption, the Iberian otter has an average need of 0.69-0.86 kg of food per day (for one sample of 39 healthy, adult and subadult individuals; Ruiz-Olmo 1995b). With fish weighing over 300 g their daily needs are clearly met with relatively few fish, and in some cases there is a greater probability that parts of the prey may be left over than if the fish weighs very little.

Several recent studies on otter diet in Iberian Mediterranean environments have reported the importance of the genera Barbus and Chondrostoma (see Ruiz-Olmo and Palazón 1997; and Ruiz-Olmo et al. in press). Barbels have a relatively high average biomass (45-300 g in our study area; Ruiz-Olmo et al. in press and J. Jiménez unpublished), they are dominant in the medium watercourses which the otter inhabits and relatively easy to catch. Their size justifies a capture rate of around 3-4 fish per hour, with an average biomass of 50-100 g. Ruiz-Olmo (1995b) estimated (with part of the data from the Pre-Pyrenees, shown here), an intake of 274 g per hour of activity, lower than the 460 g per hour estimated by Kruuk (1995) in the Shetland Islands, and a very similar value to the 290 g per hour estimated by Watt (1991) on the west coast of Scotland. According to this data, 2-3 hours of fishing daily are necessary in order to obtain sufficient food. However, variations are highlighted which could be crucial in the ecology and conservation of the species. We hope to study this topic in greater depth through future research.
Although referring to only one individual, the result obtained for 1992-93 (approximately one capture per hour), which coincided with a food shortage and a decrease in the average size and biomass of the surviving fish (Ruiz-Olmo et al. in press), is consistent with the Kruuk’s postulate (1995), who points out that otters have to prolong the amount of time spent foraging when the availability of food decreases, in order to meet the minimum requirements. During this time, the radiotracking of a wild female in the area revealed that her activity was extended on determined days by more than 16-20 hours, much longer than normal (Ruiz-Olmo et al. 1995; Jiménez et al. 1998; own unpublished observations). Therefore, the capture rate of prey should be related to the biomass and level of ease of capture, allowing for a variation for each location over time. Kruuk (1995) also demonstrates that there can be individual variations.

To conclude, the way in which fish are consumed seems to be related to their size and the parts that are most difficult to digest, which also influences which parts will be left. Research carried out along these lines is necessary if wish want to improve our understanding of the diet and energetic balance of this species.

Acknowledgements

This study has been made thanks to collaboration of numerous people in the field. We should like to thank the following people for radiotracking the otters: José María López-Martín, Alejandro Pascual, Martí Surroca, Juan José Palomo and Montserrat Sagalés. For the otter observations carried out on the riverbanks, we are grateful for the help of Santiago Palazón, José Manuel Bolado, Miquel Palacin, Vittorio Pedrocci and Oscar Arribas. For the studies on otters in captivity, we would also like to thank Javier Martínez, Jennifer Boudet, Rosa Marsol and Eva Jordà for their collaboration.

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