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WHY THE EURASIAN OTTER (*LUTRA LUTRA*) LEAVES A POND? AN OBSERVATIONAL TEST OF SOME PREDICTIONS ON PREY DEPLETION

Miguel DELIBES*, Pablo FERRERAS* & M. CARMEN BLÁZQUEZ**

RÉSUMÉ

Dans le parc National de Doñana (SW Espagne), la loutre (*Lutra lutra*) se nourrit temporairement dans divers étangs dispersés au bord des marais du Guadalquivir. D'après les analyses de 307 fèces ramassées durant trois périodes de présence de l'espèce dans un étang, nous avons étudié son régime alimentaire afin de vérifier l'hypothèse selon laquelle les loutres abandonneraient l'étang après avoir réduit la densité de leur proie favorite (anguilles de grande taille, *Anguilla anguilla*) et par conséquent seraient forcées de consommer des proies de moindre rentabilité (anguilles de petite taille et gambusies, *Gambusia affinis*). Les résultats montrent que la proportion des anguilles diminue dans le régime alimentaire de la loutre et la proportion de gambusies augmente pendant la première, et plus longue, période d'occupation de cet étang, mais non dans les deux autres cas. La diversité trophique et la taille moyenne des anguilles consommées n'ont pas changé durant la période d'étude. Nous suggérons que les changements temporaires de l'habitat et des ressources alimentaires à une échelle spatiale plus vaste pourraient expliquer les choix de la loutre mieux qu'une hypothétique densité minimale de sa proie favorite dans l'étang étudié.

SUMMARY

In the Doñana National Park (SW Spain), Eurasian Otters (*Lutra lutra*) harvest temporarily some scattered ponds close to the Guadalquivir marshes. By analysing 307 spraints collected during three periods of pond occupancy, we used the otters' diet to test the hypothesis that they leave these ponds when they have depleted their favourite prey (large Eels, *Anguilla anguilla*) and consequently are forced to eat less rewarding prey (small eels and Mosquitofish, *Gambusia affinis*). Results indicate that the proportion of eels decreased in the otter's diet, and that of mosquitofish increased, during the first and longest period of use of the pond by the otter, but not in two other instances of shorter occupation periods. Trophic diversity and average size of eaten eels did not change along the study. We suggest that temporal changes in habitat and trophic resources on a larger spatial scale could explain the decisions of the otter rather than a hypothetical giving-up density of the favourite prey in the studied pond.

INTRODUCTION

Through assuming that natural selection should favour those individuals foraging more efficiently (Valverde, 1964; Emlen, 1966), a large attention has been

* Estación Biológica de Doñana. Consejo Superior de Investigaciones Científicas, Avda. Ma Luisa s/n. Apdo. 1056. 41080, Sevilla, Spain.

** Centro de Investigaciones Biológicas del Noroeste. Apdo. 128; La Paz, 23000 Baja California Sur. Mexico.

devoted to the way individual animals adjust their foraging behaviour in response to the characteristics and distribution of their food (e.g. Kamil & Sargent, 1981). This approach allows one to generate predictions about patterns of prey and foraging patch utilization in particular situations (Pyke *et al.*, 1977; Stephens & Krebs, 1986). For instance, if we assume that trophic resources are distributed in discrete patches and that foragers deplete these resources as they harvest a patch, we can predict that a forager will maximize its rate of energy gain by leaving a patch when the harvest rate there compares badly with that of the next best patch in the range, or with the average harvest rate in the entire home range. The density in quantity and/or quality of the prey resource which leads the predator to abandon a patch has been called giving-up density (Brown, 1988).

In the Doñana National Park (SW Spain) Eurasian Otters (*Lutra lutra*) harvest discrete ponds scattered throughout the sandy scrubland. These ponds are connected among them and with the main marsh during usual winter floods, and fish (particularly Eels, *Anguilla anguilla*) stocks are replenished then. Presence of individual otters in some of these ponds may be observed for more or less prolonged periods of time, alternating with periods of absence. This situation provides a good opportunity to test some simple predictions about the factors leading the otters to leave these ponds, as these factors should be reflected in the otters' diet. Obviously, our intention is not to test any particular model of optimal foraging. This is a very difficult task to be performed in the field with an elusive carnivore such as the otter, and detailed information about abundance, profitability and the patterns of resource distribution would be needed.

Before the introduction in the area of American Crayfish (*Procambarus clarki*), otters in Doñana preyed mainly on eels, small fish less than 5 cm in length (Mosquitofish or Gambusias, *Gambusia affinis*), amphibians, and big aquatic insects (Adrián & Delibes, 1987). Where they exist, eels have been reported to be a favourite prey for the otter (Mason & Macdonald, 1986; Libois & Rosoux, 1989), while very small fish such as Gambusias are usually rejected (Kruuk & Moorhouse, 1990; Kruuk 1995; but see Libois, 1997). We assume that otters beginning to harvest a pond will prefer to capture eels to mosquitofish and also large eels to small ones (Topping & Kruuk, 1996). As the pond is being depleted of large eels, we predict that small eels and gambusias will take more importance in the diet and trophic diversity will increase, until otters cease to harvest the pond. Hence, our particular predictions are:

- a) The importance of eels in the diet will decrease from the beginning to the end of the otter's stay in a pond,
- b) simultaneously, the importance of mosquitofish and the trophic diversity will increase, and
- c) the average size of consumed eels will decrease with time spent exploiting the patch.

METHODS

The study was carried out in Lucio Bolín (37° 00' N, 6° 26' W). This is a little pond (185 × 92 m; maximum depth 110 cm; perimeter 505 m, and total surface 1.06 ha) artificially flooded throughout the year. It is situated adjoining to the main marsh of Guadalquivir River mouth, into the Doñana Biological Reserve, SW

Spain, which is flooded periodically (usually each winter; see Valverde, 1958 for a detailed description of the area). The climate is Mediterranean subhumid with Atlantic influence and a marked seasonality. Annual rainfall, about 600 mm overall, is concentrated between November and April, and the rest of the year is rather hot and dry.

Presence of otters was detected there for the first time in January 1981. Otter faeces (spraints) were collected on a monthly basis since then until July 1981, when otters disappeared. The species was detected again (and faeces collected) in November 1981, but not in December 1981. We discovered faeces again from January 1982 to March 1982, and after that, the otter disappeared at least until May 1982. In the results, the sample from February 1981 included some faeces found in January 1981, and those from January 1982 to March 1982 were pooled, because of their small monthly number.

Total number of faeces was 307, distributed in eight samples. A general picture of the otter food in Lucio Bolín based on these spraints has been presented by Adrián and Delibes (1987).

Faeces were analysed according to the method described in Conroy *et al.* (1993). The importance of each prey category in the diet was estimated from its relative frequency of occurrence, i.e. the relative contribution of each prey category to the total number of occurrences (one per category and spraint), regardless of the total number of spraints (Erlinge, 1968). Size of eels was determined from their thoracic vertebrae following Wise (1980). Significant trends in the proportion of occurrences of eels and gambusias in the diet during the occupancy months were tested using linear regression with arcsin transformed proportions over number of months since the start of the occupancy. Trends in average sizes of consumed eels during otter presence periods were tested in a similar way.

Diet diversity was measured as Levins Index (Colwell & Futuyma, 1971):

$$B = 1/\sum p_i^2 \quad (1)$$

where p_i is the percentage of occurrences of each prey type. Five types of prey were considered: eels, mosquitofish, amphibians, insects and others.

RESULTS

Eels were the main prey of otters in the area, representing 35 % of total occurrences. Their percentage of total occurrences ranged from a maximum of 48 % in November 1981 to a minimum of 24 % in June 1981. The importance of eels in the diet decreased during the first period of pond occupancy by the otter (February to July 1981; Table I), but this trend was not significant ($F = 4.64$, d.f. = 1, 4, $P = 0.098$). However, in the two other instances when an otter was detected in the pond, eels occurred in its diet in a percentage much higher than in any of the months of the longest stay (see Table I).

Mosquitofish were the second most important prey, building up to 25 % of total occurrences in the spraints and ranging monthly from 46 % in July 1981 to 18 % in the first months of 1982. In contrast with the negative trend of eels,

TABLE I

Monthly diet composition of otters as percentages of occurrences during the three periods of pond occupancy. Levins index of diversity is also shown.

| Period | Total scats | Total occurrences | Percentage occurrences | | | | | Diversity (Levins) |
|---------------|-------------|-------------------|------------------------|--------------|---------|------------|--------|--------------------|
| | | | Eels | Mosquitofish | Insects | Amphibians | Others | |
| Feb. 1981 | 72 | 153 | 39.2 | 17.6 | 17.0 | 14.4 | 11.8 | 4.0 |
| Mar. 1981 | 36 | 82 | 29.3 | 23.2 | 22.0 | 17.1 | 8.5 | 4.5 |
| Apr. 1981 | 47 | 108 | 38.9 | 18.5 | 19.4 | 12.0 | 11.1 | 4.0 |
| May 1981 | 38 | 75 | 25.3 | 25.3 | 14.7 | 14.7 | 20.0 | 4.7 |
| Jun. 1981 | 21 | 51 | 23.5 | 27.5 | 13.7 | 15.7 | 19.6 | 4.7 |
| Jul. 1981 | 35 | 68 | 26.5 | 45.6 | 16.2 | 2.9 | 8.8 | 3.2 |
| Nov. 1981 | 37 | 61 | 47.5 | 34.4 | 8.2 | 3.3 | 6.6 | 2.8 |
| Jan-Mar. 1982 | 21 | 34 | 47.1 | 17.6 | 23.5 | 5.9 | 5.9 | 3.2 |
| Total | 307 | 632 | | | | | | |
| Average | | | 34.7 | 26.2 | 16.8 | 10.7 | 11.5 | 3.9 |

gambusias in the otter diet significantly increased during the first and longest period of occupancy of the pond ($F = 10.13$, $d.f. = 1, 4$, $P = 0.33$; Table I). The ratio of eels to mosquitofish significantly decreased during the first period of occupancy ($F = 8.99$, $d.f. = 1, 4$, $P = 0.04$; Fig. 1), but not during the other periods, with the value during January-March 1982 being the highest during the study (2.67; Fig. 1).

The average size of eels was very similar in all the monthly samples, ranging from 37.4 ± 1.7 to 32.5 ± 1.4 cm (Fig. 2). No significant trend was found during the months of occupancy ($F = 0.029$, $d.f. = 1, 4$, $P = 0.87$, between February and July 1981), and we were unable to detect a decrease in the size of the captured eels during the stay of the otter in the pond.

There was no significant trend in diet diversity between February and July 1981 ($F = 0.264$, $d.f. = 1, 4$, $P = 0.635$), although diversity was the lowest in the month of the otter's disappearance (Table I). During the two other shorter periods of otter occupancy of the pond (November 1981 and January-March 1982), diversity remained lower than in the first part of its stay (Table I).

DISCUSSION

Although frequently used (see Conroy *et al.*, 1993), our methods to estimate the proportion of eels and gambusias in the diet and the sizes of eels could represent serious shortcomings of the results. Recently Carss & Parkinson (1996) concluded it is not possible to quantify otter diet accurately by frequency of occurrence methods. However, they and some other authors (e.g. Beja, 1997) found a close correlation between frequency of occurrence and biomass proportions in the diet, the main deviations corresponding to the rare items. To avoid this

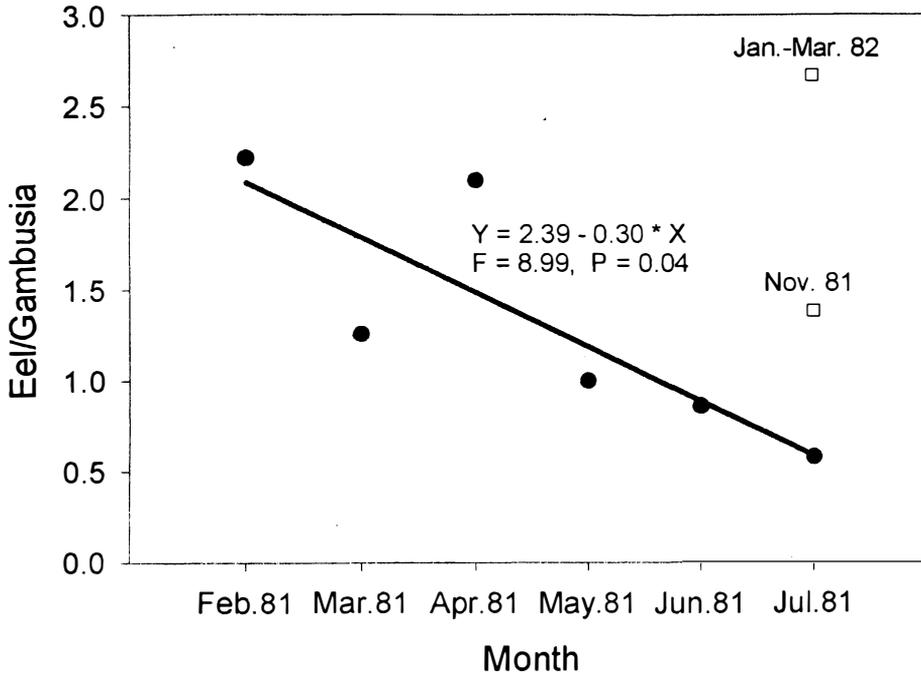


Figure 1. — Proportion of eels to gambusias in the otter diet (as percentage of occurrences in spraints) in monthly samples during the study. The decreasing trend during the first period of occupancy (February-July 1981), depicted by circles, is significant ($F = 8.98$, $P = 0.04$) and the figure shows the fitted line. Squares indicate the proportions for the later periods of pond occupancy by the Otter (November 1981 and January-March 1982).

problem we considered in our analysis only the two commonest items (eels and gambusias) and we did not try to make a detailed description of the otter diet. Hence, we think our results are acceptable. Also, Carss & Elston (1996) proved that the method we used to estimate eel sizes overestimated the proportion of small individuals. However, we expected similar potential biases in all months and so a change in the mean size of the eaten eels should be detected.

Our predictions were only partially fulfilled by data, which is rather common when testing in the field foraging models which aim for generality rather than precision (Stephens & Krebs, 1986). From our results it is suggested that the energy gain of eels per hunting effort decreased from February to July 1981, and as a consequence more and more small fish were eaten. This is even clearer from the changes in the proportion from eels to gambusias in the analysed spraints (Fig. 1) and could explain why the otter left the pond. Proportions of eels were high again when the otter returned in November 1981 and January 1982, suggesting the pond was replenished with eels during the winter flooding of the adjoining marsh. However, the otter left the pond again almost immediately (Fig. 1).

We have analysed only the proportions of eels and gambusias in the diet in order to reduce potential methodological biases (see the beginning of this

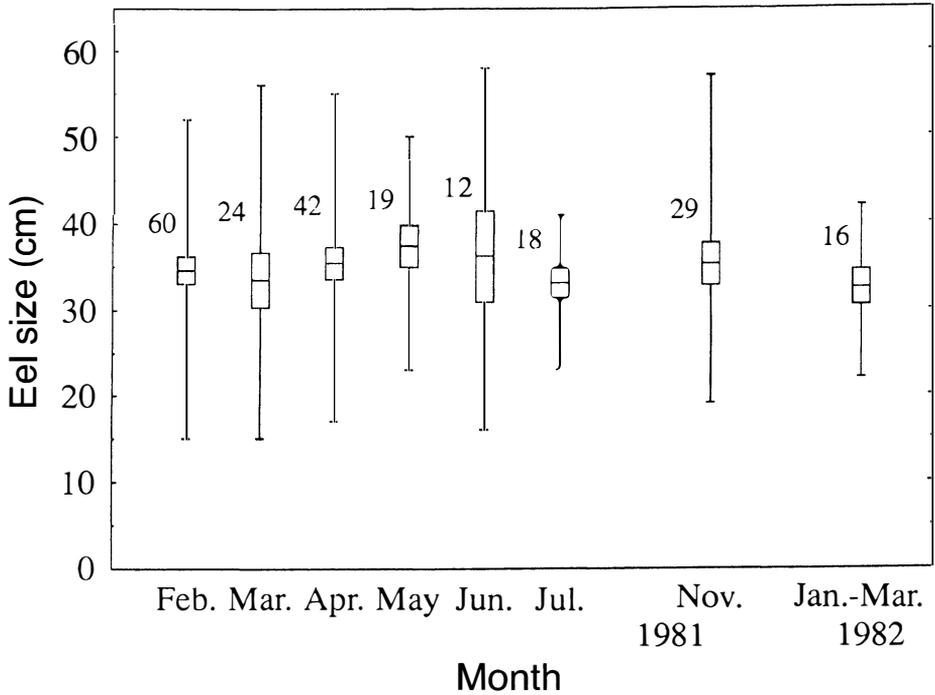


Figure 2. — Size of eels captured by otters during the study, as estimated total length from size vertebrae found in otter spraints. Mean \pm standard error (boxes) and extreme values (segments) for each monthly sample (number above each box).

Discussion). However, the role of some other prey could be also important. Insects must be considered “less rewarding prey” and their role in the otter food in our pond seems to be moderately constant along the time. On the contrary, amphibians may be an energetically important food for otters (Sidorovich & Pikulik, 1997), especially in southern areas (e.g. Callejo, 1988; Ruiz-Olmo & Palazón, 1998), and by the time the otter left the pond their role as prey sharply dropped or was very low (Table I). Moreover, the relative importance of amphibians in the diet could be underestimated by our method of prey quantification (Beja, 1996). Hence, we cannot discard the possibility that otter leaves the pond when the availability of amphibians is low.

An alternative explanation for our results is that the otter was not a selective predator (i.e. it made a random choice of prey). In this case eels would not be depleted before other prey items, as all of them would be eaten when found. Simply, the otter would go to hunt elsewhere when the rate of prey encounter in the pond decreased below a threshold (the giving-up density; Brown, 1988; Hugues & Ward, 1993). We are not able to test this possibility, as we recorded the proportions of prey in the otter’s diet, but not the actual number of found and/or consumed prey.

Our data do not reflect a complete selectivity for eels, as in this case only eels, as the highest ranking prey, should be eaten and the low ranking prey (mosquitofish) ignored, according to the predictions of the classical optimal foraging models (Stephens & Krebs, 1986). However, such partial preferences are commonly found in studies of prey choice and do not necessarily show a lack of selectivity (Krebs & Kacelnik, 1991). Moreover, different authors (Libois & Rosoux, 1989; Kruuk, 1995) agree that otters prefer eels when available and several studies suggest that suboptimal prey consumption by otters would be highest (and also natural mortality) when availability of optimal prey is low (Kruuk & Conroy, 1991 in coastal habitats; Kruuk *et al.*, 1993 in freshwater habitats).

Likewise, a lack of selectivity upon eel size could explain why the size of the eaten eels did not diminish with the residence time of the otter in the pond. Wise *et al.* (1981) found no evidence of selection on prey size in 4 fish species. Also, Libois & Rosoux (1989) found no evidence of selection in the size of eels captured by otters in the Marais Poitevin of western France. On the contrary, Beja (1997) found a selection of the largest fish species by marine-feeding otters in South Portugal, and Topping & Kruuk (1996) showed that captive otters were able to discriminate even between rather similar sized eels, selecting usually the longer ones.

A different explanation would be that fish removed by otter were replaced by others within a short time, as indicated by Kruuk *et al.* (1988) for coastal habitats. However, this possibility is very scarce in a pond isolated from the main marsh most time of the year (except if there were fish refuges inside the pond not exploited by Otters).

A third explanation refers to spatial scale problems. It is likely that the otter does not use exclusively the pond when it is detected there, but a larger area which includes several ponds. In this case, we must assume that scats would reflect the diet, and food should be depleted, in that larger area, which was actually left by the otter. However, at this scale the area could be left by reasons not directly related to local food availability. In fact, when the otter left the pond in the first instance (July 1981) the marsh and most of the temporal lagoons were dry and the flooded study pond probably was too small and distant from other food patches to be usefully exploited. The otter returned to the pond following the first annual rains in October 1981, but left it again at the end of November, when generalized rains have flooded most of the area. Also, in this case the marginal value theorem suggests that residence time in a patch will be shortened when the travel time to another patch diminishes (Charnov, 1976). The otter returned in January, coinciding with a decrease of flooding, and left in April 1982, when most of the area (but not the study pond) was dry again. These results suggest that for unknown reasons the study pond should be exploited by otters mainly in intermediate situations between general flooding and general drought in the whole region. In this context it should be necessary to consider the missed opportunity costs, i.e. the cost of foraging in the study pond and not in other places which could have better conditions (Brown, 1988).

Finally, several hypotheses related with social behaviour, breeding conditions, seasonal increase of risks, etc., could be also invoked to explain why our predictions were not completely met. Hence, we must conclude that factors affecting otter foraging decisions in the field are complex and often inter-related, in need of more research.

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