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Desert otters: Distribution, habitat use and feeding ecology in arid rivers of Morocco

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ABSTRACT

Some of the most arid environments inhabited by the Eurasian otter (*Lutra lutra*) are the river systems draining the southern slopes of the High Atlas Mountains into the Sahara Desert, where we have studied otter distribution, habitat use and feeding ecology. We found signs of otter presence in 61% of 80 sampled sites. The species was widespread at intermediate elevations within the study area, being rarer at high altitudes (above 2000 m a.s.l.) and, especially, in the arid lowlands. The intensity of habitat use, estimated from spraint counts, also peaked at intermediate elevations. Otter diet, described through the analysis of 554 spraints, was dominated by fish in general (found in 97% of the sprains) and *Luciobarbus* barbels in particular (86% of spraints). The otter positively selected barbels of intermediate sizes (100–160 mm in length), avoiding the smallest size classes and consuming larger ones according to their availability. Our results suggest that otter may be vulnerable to the harsh environmental conditions in arid areas. This aridity-driven vulnerability is expected to increase in the area and to expand to other peri-Mediterranean regions in the future.

1. Introduction

Arid or semi-arid areas cover around 30% of the global land surface (Safriel and Adeel, 2005) and are expanding as a consequence of climate change (Cherlet et al., 2018). These areas include, either totally or partially, a prominent component of the world's river systems, but arid rivers have been much less studied than rivers in wetter regions (Harms et al., 2008), despite being more diverse in their hydrological and physicochemical characteristic (Kingsford and Thompson, 2006). Arid areas host specialized biotas with complex evolutionary histories, but they also constitute distribution limits for the biota of surrounding wetter biomes, thus acting as border areas (Goodall, 2014). This is the case of the Sahara Desert, which constitutes an extreme, though highly dynamic barrier between the Afrotropical and Palearctic realms (Le Houérou, 1992; Drake et al., 2011; Brito et al., 2014). As a result, North-western Africa hosts organisms of diverse biogeographical affinities, both in terrestrial (Dobson and Wright, 2000; Leite et al., 2015) and aquatic environments (Lévêque, 1990; Clavero et al., 2017).

The Eurasian otter (*Lutra lutra*, henceforth simply the otter) is one of the many species with a distribution limit in the arid regions of North-western Africa. The otter has a very wide range, covering most of the Palearctic and part of the Indo-Malay biogeographic realms, with the Sahara Desert constituting the South-western limit (Roos et al., 2015, Fig. 1A). This species is strictly linked to aquatic systems, as it feeds exclusively on aquatic or semiaquatic prey (e.g. Clavero et al., 2003), and would arguably be limited by the scarcity or lack of superficial water in arid environments. In spite of this, across its vast distribution range, the otter inhabits several arid and semiarid areas (Neronov and Borbrov, 1990; Reuther et al., 2000; Karami et al., 2006; Valera et al., 2011). However, little is known about the otter in such arid environments. Most of the studies on the distribution, status and ecology of the otter have been developed in Europe, where the otter became a flagship species for conservation after its drastic decline during the second half of the 20th century (e.g. Cianfrani et al., 2011). Contrastingly, the knowledge of the otter in Northern Africa is in general scarce (Libois et al., 2015b), and more even so in the most arid areas of this region.

During the early 1980s Sheila Macdonald and Chris Mason travelled Morocco, Algeria and Tunisia in search of otters, reporting the first

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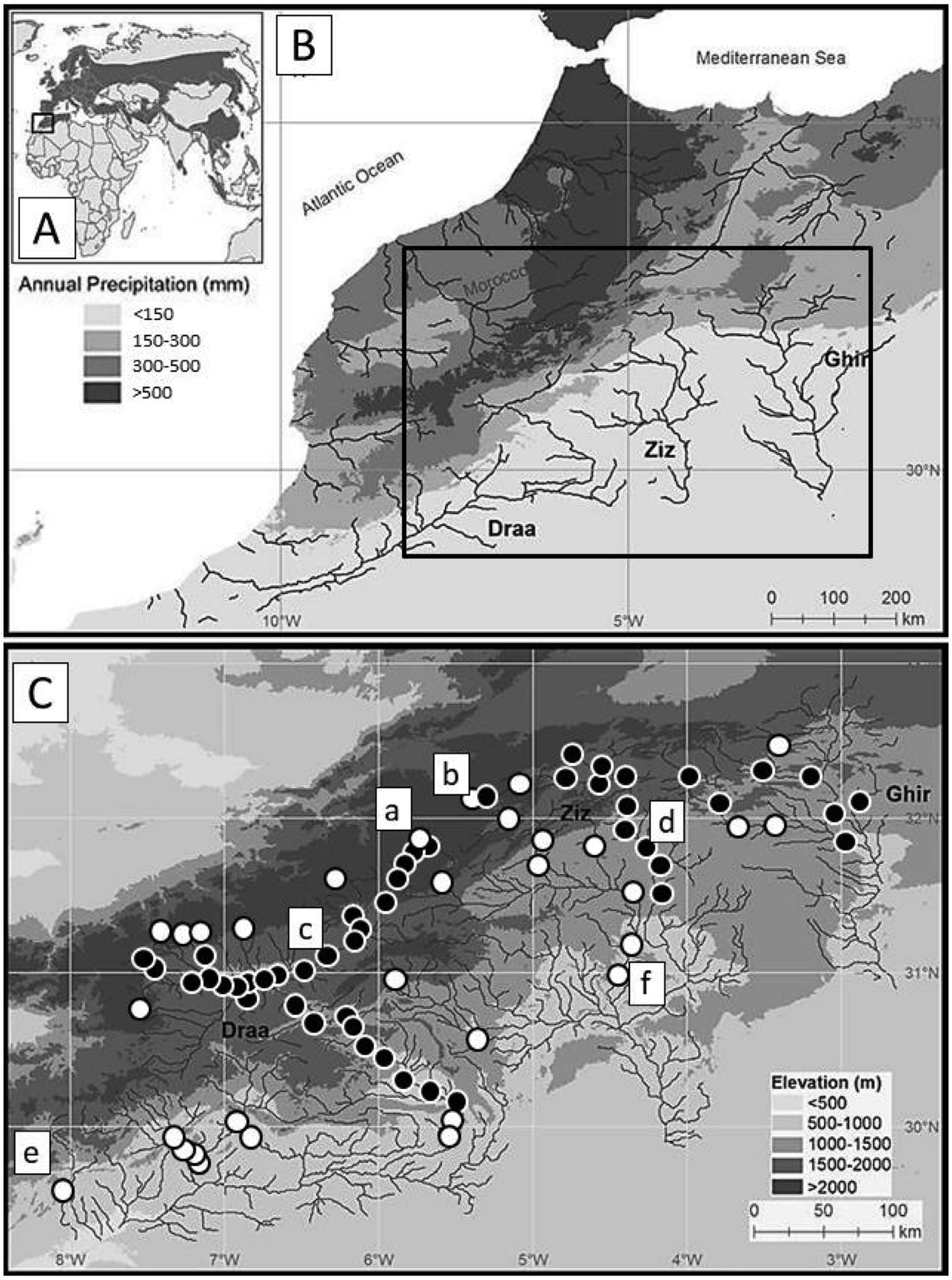

Fig. 1. A: Global distribution of the Eurasian otter (*Lutra lutra*), as reported by the IUCN Red List (iucnredlist.org). The rectangle shows the area enlarged in B. B: situation of the three studied river basins in northern Africa with a background pattern informing about the variation in average annual precipitation. The rectangle marks the area enlarged in C. C: Otter distribution in the study area (black dots denote presences, white dots denote absences), with a background pattern informing about elevation. Lower case laters identify the sites illustrated in Fig. 2.

systematic information on the distribution of the species in Northern Africa (Macdonald & Mason, 1983, 1984; Macdonald et al., 1985). Their work in Morocco (Macdonald and Mason, 1984) covered mainly the western part of the country and did not include the river basins draining south of the High Atlas mountain range, which are amongst the driest ones hosting otters within the otter range. Broyer et al. (1988) expanded the work of Macdonald and Mason (1984) on otter distribution, providing data from river systems flowing into the Mediterranean Sea and from those of the most arid areas of Morocco, including oueds (= rivers) Draa, Ziz and Ghir, the most important pre-Saharan river systems draining the High Atlas mountain range (Clavero et al., 2017). Even though there have been recent studies on otter distribution (Delibes et al., 2012) and trophic ecology (Libois et al., 2015a,b) in Northern Africa, the species has not been studied again in arid Morocco since the 1980s. Revisiting the status of the otter in these arid environments is interesting to evaluate whether it has remained stable, as reported for western Morocco (Delibes et al., 2012), has improved, as in semi-arid Mediterranean regions of Europe (Clavero et al., 2010; Balestrieri et al., 2016), or has worsen, a situation that could be linked to the extreme environmental conditions. Understanding otter ecology in arid environments may be also useful to predict how otter populations may respond to the forecasted increases in aridity in many areas inhabited by the species (e.g. Van Dijck et al., 2006; Cianfrani et al., 2011).

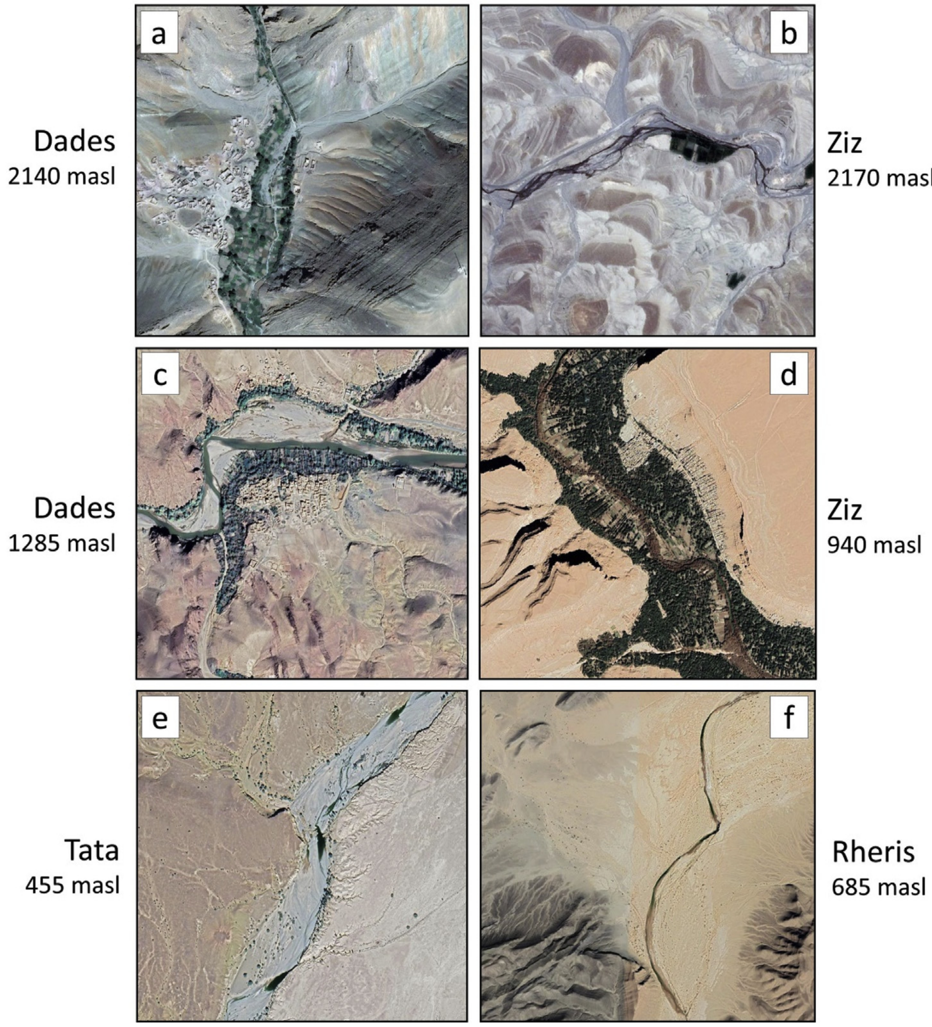

Fig. 2. Aerial images of six of our sample sites, identifying the name of the water course and the elevation of the stretch, taken in the river channel. Letters correspond to those provided in panel C of Fig. 1.

Thus, we analyzed spatial patterns in distribution, habitat use and diet composition of the otter in oueds Draa, Ziz and Ghir. These basins embrace steep environmental gradients ranging from cold and relatively humid high-mountain environments to extremely dry lowlands (Schulz and Judex, 2008, Fig. 2). We assessed how the otter copes with this enormous environmental variation, which has a critical influence on potential prey (Clavero et al., 2017, 2018) and may involve limitations for otter presence at both of its extremes. Specifically, we: i) describe otter distribution and analyze the factors that may determine it; ii) assess habitat use by spraint (i.e. faeces) counts (see Hong et al., 2020); and iii) report otter diet composition and its variation along environmental gradients.

2. Materials and methods

2.1. Study area

The study was carried out across the basins of oueds Draa, Ziz and Ghir. Annual precipitation is relatively high in high-altitude areas, reaching around 500 mm at 3000 m a.s.l., but steeply decreases towards lower lands, being lower than 100 mm at 1000 m a.s.l. (Schulz and Judex, 2008, Fig. 1B). In those lower areas annual precipitation is also more unpredictable (Schulz and Judex, 2008) and water salinity is higher (Clavero et al., 2015).

Oued Draa is the longest river in Morocco, with a total length of about 1100 km. Its main sources are oueds Dades and M'Goun and it flows into the Atlantic Ocean near the city of Tan-Tan (~28.7°N; 11.1°W). Superficial water flow in Oued Draa usually disappears some 600 km upstream from the estuary, and middle stretches of the river connect with the estuary only during extreme rain episodes (Dłużewski and Krzemień, 2008). Oueds Ziz and Ghir flow in a dominant southward direction, directly to the Sahara desert, and thus have no connection to the sea. These rivers formed part of one of the endorheic mega-lake systems that characterized the now desert Saharan area during wetter periods (Drake et al., 2011).

2.2. Field sampling

Field sampling was carried out in March and April 2013. Overall, we sampled 80 sites for signs of otters (tracks and spraints) along 600 m of riverbank at each site. Otter spraints are easily identified through their characteristic aspect and smell and easily found because they are deposited in prominent places within the river bed or at its banks. We considered a site as positive whenever we found at least one otter sign, and as negative otherwise. This approach assumes that if no otter sign is found in 600 m there is a very small probability of finding them with longer transects (Macdonald, 1990). The number of otter spraints is often interpreted as an index of population abundance and habitat use, referred to as marking intensity (Mason and Macdonald, 1987). Even though the interpretation of marking intensity has been controversial

(Kruuk and Conroy, 1987), recent work supports the usage of this index as an indicator of otter population status (Hong et al., 2020). Thus, we counted the number of otter spraints in all positive transects, in order to calculate an index of marking intensity (number of spraints × 600 m^{-1}). In order to frame the marking intensity figures obtained in our study area, we reviewed values of marking intensity for other places in Europe and Northern Africa reported in scientific articles, transforming the reported values to 600 m transects whenever it was necessary. We followed the approach of Mason and Macdonald (1987) and related the marking intensity recorded in each area with the percentage of positive otter sites in that area. We then checked whether the values obtained in our study area fitted in that relationship or departed from the general pattern.

We surveyed fish communities in order to estimate the availability of potential prey. Whenever possible, we used a portable electrofishing device (model HI ELT60 II, Hans Grassl GmbH, KONIGSSEE, Germany) along approximately 100 m river stretches (111 m average, range 39–400 m). Electrofishing sessions comprised a single pass, did not imply net blocking of rivers and used pulsed direct current (50–75 pulses/second). This fish sampling procedure was applied for 62 sites, but was not possible in the remaining 18 sites, mainly due to high water conductivity (over 6000 μS/cm; see Clavero et al., 2015). When electrofishing was not feasible, we used fyke and seine nets. We set two types of fyke nets, with different mesh sizes (3.5 and 7 mm), for 24 h. The seine net employed was 5 m-long and 1.5 m-high and had a mesh size of 4 mm (Clavero et al., 2017). We measured the total length of all captured fish to the nearest millimeter.

We recorded 16 variables to characterize the environmental variability of river habitats, including data related to physicho-chemical water characteristics and the structure of river bed and banks (Table 1). All environmental variables were collected in the field, with the exception of altitude, which was calculated using GIS. Physicho-chemical parameters were recorded just once at each site, but the rest of environmental variables were measured or estimated several times, by setting transects (on average 4 transects, range 1–6) perpendicular to water flow, separated 20 m one from each other. For some of them (e.g. water depth and velocity, substrate size) we took measures three times at each transect (approximately at 25%, 50% and 75% of the river width). The values of all field-recorded variables were then averaged to characterize sites, with the exception of maximum depth, which was the maximum among the recorded values.

Table 1
Environmental variables recorded for every sampled site, indicating their units and, when necessary, the transformation applied prior to numerical analyses. The loadings of each variable for the three principal components (PCs 1 to 3) extracted from the principal component analysis are also shown (values equal or larger than 0.5 in absolute value are highlighted in bold), as well as the eigenvalues associated to each PC and the percentage of the variability of the original dataset explained by them. Values of categorical variables as follows: * Cover, field estimate, in categories ranging between 0 and 4: 0 (0%), 1 (0–25%), 2 (25–50%), 3 (50–75%, 4 (75–100%); **Dominant substrate categories ranging between 1 and 8: 1 (silt and clay), 2 (sand), 3 (heavy sand), 4 (gravel), 5 (heavy gravel), 6 (stone), 7 (heavy stone) and 8 (bedrock); *** Water speed estimated in three categories, between 0 and 2: 0 (no current), 1 (slow current) and 2 (fast current).

	Units	Transf.	PC1	PC2	PC3
Conductivity	S/cm	$Log_{10}(X)$	**0.88**	−0.13	0.12
Water temperature	°C	X^2	**0.77**	0.20	0.08
Dissolved oxygen	mg/l		0.49	0.06	0.36
pH		X^2	−0.19	−0,13	−0.37
Aquatic Vegetation	Cat*		**0.50**	0.45	0.06
Riparian trees	Cat*	$Log_{10}(X)$	−0.41	**0.55**	0.13
Riparian bush	Cat*	√X	0.31	**0.72**	0.09
Riparian herbaceous	Cat*	$Log_{10}(X)$	−0.23	**0.56**	0.21
Riparian rock	Cat*	$Log_{10}(X)$	0.04	**−0.75**	0.06
Width	m	√X	0.18	0.15	**0.59**
Average depth	cm	√X	0.24	0.04	**0.87**
Maximum depth	cm		0	0.06	**0.91**
Substrate	Cat**	X^2	**−0.63**	0.20	−0.16
Speed	Cat***		**−0.84**	0.02	−0.21
Altitude	m		**−0.85**	0.11	−0.35
Eigenvalue			4.12	2.06	2.47
% Variance			0.27	0.14	0.16

2.3. Diet analysis

We collected 554 otter spraints from 34 sites to analyze the composition of otter diet and its spatial variability. In the laboratory, otter spraints were soaked for at least one day in soapy water and then filtered through a 0.325 mm mesh. Prey remains were identified using a binocular microscope, aided by published keys (Felix and Montori, 1986; Prenda et al., 1997; Miranda and Escala, 2002; Blain et al., 2008). The identification of a given prey type in a spraint was considered an occurrence and diet composition was expressed as frequency of occurrence (FO, number of occurrences of a certain prey type divided by number of spraints analyzed). To ease the comparisons with other studies, we also reported diet composition in terms of relative frequency of occurrence (RFO, number of occurrences of a certain item as percentage of the total number of occurrences of all prey items) (Clavero et al., 2003).

Barbels (genus *Luciobarbus*) are the most abundant and widespread fish in our study area (Clavero et al., 2017). Thus, we initially assumed that they would be a relevant otter prey and further analyzed barbel consumption. The minimum number of barbel individuals in each analyzed spraint was estimated from the number and position (right-left) of key diagnostic bones, such as premaxillae, maxillae, dentary and pharyngeal teeth. These key structures were measured in order to estimate the size of consumed barbels by otter. Since we did not have retrocalculation equations to estimate the original size of Moroccan *Luciobarbus* barbels from these key bones, we used the equations published for Iberian congeneric species (Prenda et al., 2002; Miranda and Escala, 2002). The size of each individual was estimated for every key structure using all available equations for Iberian *Luciobarbus*, and then averaged to obtain our final size estimate.

2.4. Statistical analyses

We performed a principal component analysis (PCA) to summarize the variability of the original set of 16 environmental variables in a reduced number of ecologically meaningful gradients. Prior to the PCA, we transformed those variables that departed strongly from a normal distribution (Table 1). To facilitate the interpretation of the resulting PCs, we performed a varimax orthogonal rotation, after selecting the most appropriate number of PCs by attending at the eigenvalue sedimentation graph (i.e. scree-plot criterion; McGarigal et al., 2000). The first three principal components (PC1, PC2 and PC3) accounted for 57.7% of the variation of the original dataset (Table 1). PC1 described an altitudinal gradient running from upstream to downstream river sections, integrating changes in elevation, water conductivity and temperature and water speed, among other features. PC2 described a riparian vegetation gradient, varying from sites with relatively high tree, shrub and herbaceous cover to sites with bare river shores. PC3 represented a gradient related to the width and depth of river stretches.

We studied the environmental constraints of otter distribution in the study area by analyzing the influence of the three extracted PCs on the presence or absence of the otter, by means of generalized linear models (GLMs) with binomial distribution and logit link function. To assess the variability in the intensity of habitat use we selected only positive sites and analyzed the influences of the PCs on marking intensity using GLMs with Poisson distribution and log link function. In both cases, we followed a sequential backward procedure to select the final explanatory variables included in the models. First, we run a full model, including all explanatory variables (PCs) and their quadratic terms, in order to allow unimodal relationships between environmental gradients and otter distribution. Then, we removed non-significant ($P > 0.1$) terms, first the quadratic terms and then the PCs, provided that the correspondent quadratic term had already been removed. We followed this same model selection approach to relate the FO of the main prey types (fish and amphibians) and the average size of consumed barbels to the environmental gradients represented by the PCs, in these cases using GLMs with normal distribution and identity link function.

To analyze possible preferences for specific barbel sizes, we compared the sizes of available and consumed barbels using the Ivlev's electivity index, as modified by Jacobs (1974). To do so, we classified barbels (either available or consumed) into 10 size-classes, in 20 mm intervals and applied the following formula

$$D_i = (r_i - p_i) / (r_i + p_i - 2r_ip_i)$$

where D_i is the otter electivity for size-class i, r_i is the proportion of consumed barbels in size-class i and p_i is the proportion of available barbels in size-class i. The electivity estimate (D_i) ranges from −1 (total avoidance of that size-class) to 1 (absolute preference for that size class), with values around zero denoting random use. We calculated the average D values for each barbel size class across sites and assessed whether their associated 95% confidence intervals included zero or not, denoting no electivity and significant avoidance or preference, respectively. Before doing this averaging, in every site we excluded those size classes that were not captured in the field (i.e. $p_i = 0$).

3. Results

3.1. Distribution and habitat use

The otter was present in the three studied river basins, being recorded in 49 of the 80 sampled sites (i.e. 61%) (Fig. 1C). The species occurred mainly on the main water courses within each basin, being absent on medium-sized tributaries such as oueds Tissint and Zguid, right margin tributaries of the middle Draa, and Oued Rheris. The otter was also absent in the lowest studied reaches of the Draa and Ziz basins, although it was present in the lowest reaches surveyed within the Ghir basin. Marking intensity in positive sites varied between 1 and 99 spraints per 600 m (mean = 23.9; median = 17). Marking intensity values reported in the literature for 25 areas in Europe and Northern Africa were positively related with the proportion of positive otter sites in those same areas, and the figures observed in our study area fitted well in this relationship (Fig. 3).

The probability of otter presence followed unimodal relationships with all three PCs (Table 2), although it tended to be higher towards the negative end of PC1 (higher areas), and towards the positive extremes of both PC2 (vegetated banks) and PC3 (larger water systems). Marking intensity, analyzed using only presence sites, followed a unimodal pattern along PC1 similar to that of otter presence, while was positively, though weakly, related to PC2. Marking intensity had an inverse unimodal relationship with PC3 (i.e. positive estimate for the squared term, involving higher values at the gradient's extremes, see Table 2). Both otter presence and marking intensity showed strong unimodal relationships with elevation (Fig. 4). The probability of otter presence peaked at elevations between 1200 and 1400 m a.s.l., sharply decreasing upstream and downstream. The highest marking intensity values were recorded at somehow lower elevations, around 1000–1200 m a.s.l., and the decline in this indicator of habitat use was more clear upstream than downstream. We detected signs of otter presence on only three out of seven sites over 2000 m a.s.l., up to a maximum of 2127 m a.s.l., and always in very small numbers (one or two spraints per site). On the other hand, the otter was absent at elevations below 600 m a.s.l.

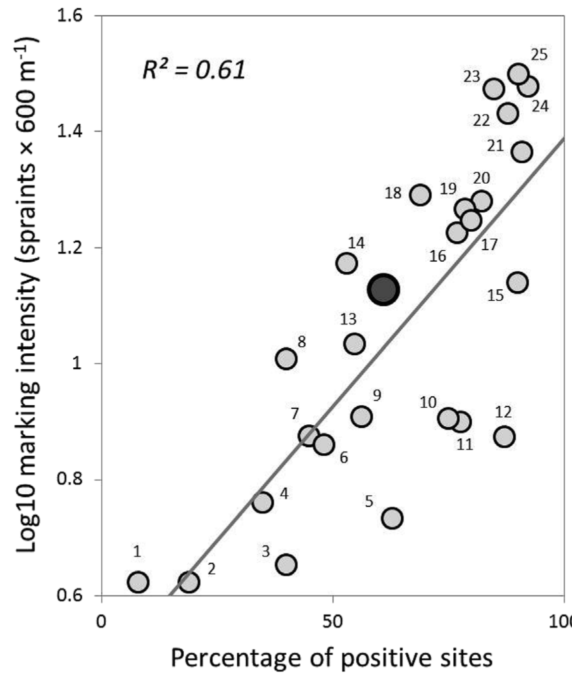

Fig. 3. Relationship between the percentage of positive sites and the mean marking intensity, reported for 25 otter surveys. The large, dark dot marks the figures obtained in this study and is not included in the calculation of the regression line. Sites location and sources: 1- Italy (Mason and Macdonald, 1987); 2- Algeria (Mason and Macdonald, 1987); 3- Spain (Mason and Macdonald, 1987); 4- southern Albania (Hysaj et al., 2013); 5- central Wales (Mason and Macdonald, 1987); 6- western Poland (Romanowski, 2013); 7- western Morocco (Mason and Macdonald, 1987); 8- Tunisia (Mason and Macdonald, 1987); 9- central Greece (Mason and Macdonald, 1987); 10- southern Italy (Fusillo et al., 2007); 11- Sele basin, Italy (Fusillo et al., 2007); 12- northern Poland (Romanowski, 2013); 13- Albania (Prigioni et al., 1986); 14- Alento basin, Italy (Fusillo et al., 2007); 15- Drina river, former Yugoslavia (Taylor et al., 1988); 16- Semani river, Albania (Bego et al., 2011); 17- Segura basin, Spain (Dettori et al., 2019); 18- Portugal (Mason and Macdonald, 1987); 19- Calore basin, Italy (Fusillo et al., 2007): 20- Pollino National Park, Italy (Prigioni et al., 2005); 21- Guadalete river, Spain (Prenda and Granado-Lorencio, 1996); 22- Andalucía, southern Spain (Mason and Macdonald, 1987); 23- Pelopponese, Greece (Mason and Macdonald, 1987); 24- Thrace, Greec (Mason and Macdonald, 1987); 25 eastern Poland (Romanowski, 2013).

Table 2
Final models describing the influence of the main environmental gradients in the study area (see Table 1) on otter distribution (i.e. presence/absence) and marking intensity (i.e. number of spraints found in 600 m transects) in positive sites. The squared PC2 (sqPC2) was deleted from the marking intensity model due to non-significance ($P > 0.1$; see methods for model selection procedures). For each model, the percentage of explained deviance is reported as a measure of effect size. Significance codes: ***P < 0.001; **P < 0.01; *P < 0.1.

	Predictors	Estimate	P
Distribution	Intercept	−8.3	**
28.5% explained deviance	PC1	2.6	*
	PC2	3.1	*
	PC3	3.2	*
	sqPC1	−0.9	**
	sqPC2	−0.5	*
	sqPC3	−0.5	*
Marking intensity	Intercept	3.09	***
9.3% explained deviance	PC1	1.09	***
	PC2	0.09	*
	PC3	−0.83	***
	sqPC1	−0.29	***
	sqPC3	0.17	***

Code of significance: 0 '***' 0,001 '**' 0,01 '*' 0,05 '.' 0,1 '' 1.

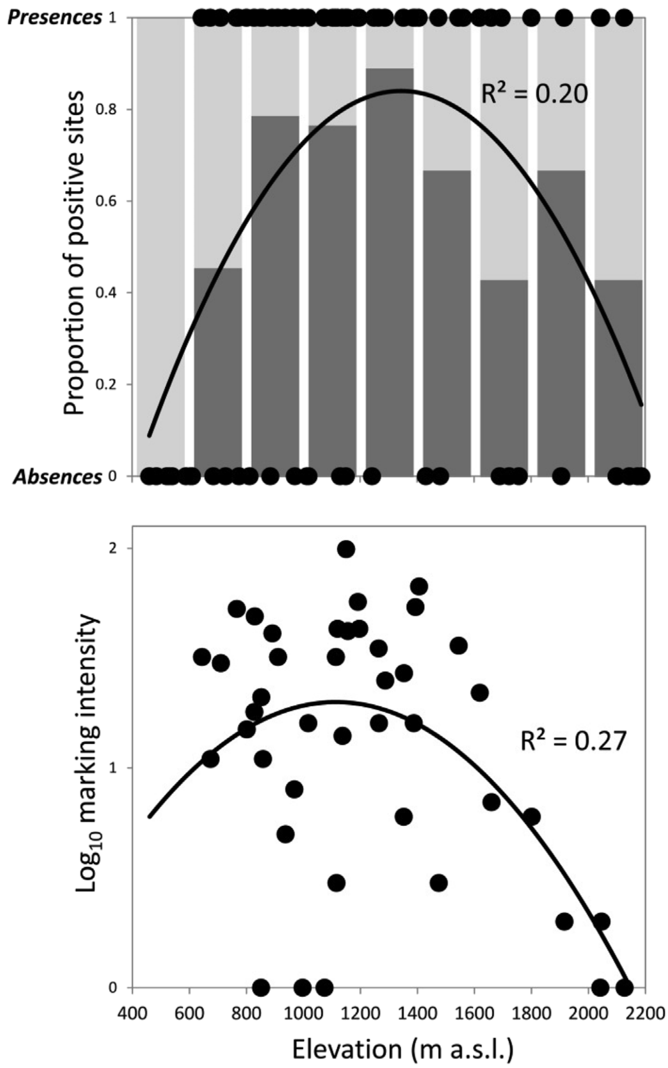

Fig. 4. Unimodla relationships between elevation and the presence or absence of otters (above) and marking intensity (i.e. number of otter spraints found in 600 m transects) (below). In the upper panel background columns show the proportion of positive (dark grey) and negative (light grey) sites in 200 m elevation classes.

3.2. Patterns in diet composition

Fish was the most important prey of the otter in the area. We found fish remains in 90% of the sites and in the vast majority (97%) of spraints analyzed. Fish made up more than 75% of the total occurrences (Table 3). Amphibians and reptiles were the only relevant alternative prey, their remains being found in two thirds and one third of the sites and in 23% and 5% of the spraints, respectively. Birds and insects were occasional prey (Table 3).

Luciobarbus barbels were the most commonly consumed fish (FO = 85%; Table 3). Other fish prey were non-natives pumpkinseed sunfish (*Lepomis gibbosus*) and big-scale sand smelt (*Atherina boyeri*) and the Afrotropical relict bluetilapia (*Oreochromis aureus*). The Sahara frog (*Pelophylax saharicus*) was the most consumed amphibian. Other amphibian prey included Bufonidae toads (which may include *Amietophrynus mauritanicus*, *Barbarophryne brongersmai* and *Bufotes boulengeri*, and maybe *Bufo bufo* in high elevation areas) and only occasionally the Mediterranean tree frog (*Hyla meridionalis*) and Moroccan painted frog (*Discoglossus scovazzi*).

The FO of fish in otter spraints was higher at lower elevation (higher PC1 values), while that of amphibians followed the contrary pattern, increasing at higher altitudes (Table 4). Fish consumption was also larger in larger water systems, as shown by its positive relation with PC3. The otter consumed barbels across a wide range of sizes, between 32 mm and 477 mm (mean = 104 mm; median = 95 mm; Fig. 5A). The average size of consumed barbels increased downstream and with the size of water systems (positive relationships with PC1 and PC3, respectively, Table 4). There was a positive relationship between the average sizes of available and consumed barbels in the different electrofished sites, although the latter tended to be on average larger than the former, this being the case in 25 out of 28 sites (Fig. 5B). The analysis of the electivity of different size classes showed that the otter avoided individuals smaller than 80 mm and positively selected individuals between 100 and 160 mm in length (Fig. 5C). Individuals between 80 and 100 mm and those larger than 160 mm were not significantly avoided or preferred.

Table 3
Composition of otter diet in the study area, expressed as the percentage of sites where each prey type was identified, frequency of occurrence (FO) and relative frequency of occurrence (RFO).

	% Sites	FO	RFO
Fish	**88.6**	**97.5**	**75.9**
Luciobarbus sp.	81.8	85.7	66.8
Atherina boyeri	9.1	1.6	1.3
Lepomis gibbosus	15.9	4.3	3.4
Oreochromis aureus	6.8	1.4	1.1
non-identified cyprinid	15.9	4.3	3.4
Amphibians	**65.9**	**23.3**	**18.1**
Pelophylax saharicus	56.8	18.0	14.1
Fam. Bufonidae	27.3	4.3	3.4
Hyla meridionalis	6.8	0.5	0.4
Discoglossus scovazzi	2.3	0.4	0.3
NI amphibian	6.8	0.5	0.4
Reptiles	**31.8**	**5.4**	**4.2**
Mauremys leprosa	20.4	2.9	2.2
Natrix maura	18.2	2.5	2.0
Birds	**9.1**	**1.3**	**1.0**
Insects	**2.3**	**0.3**	**0.3**

Table 4
Final models describing the influence of the main environmental gradients in the study area (see Table 1) on different descriptors of otter diet, namely the frequencies of occurrence (FOs) of the main prey types (fish and amphibians) and the average estimated size of the barbels consumed at each site. The percentages of explained deviance are reported as a measure of effect size. See methods for model selection procedures. Significance codes: ***P < 0.001; **P < 0.01; *P < 0.1: ns P ≥ 0.1

	Predictor	Estimate	P
FO Fish	Intercept	24.8	ns
23.6%	PC1	17.0	**
	PC3	11.3	*
FO Amphibians	Intercept	49.0	***
27.4%	PC1	−15.4	***
Size of consumed barbels	Intercept	66.7	***
20.0%	PC1	13.7	*
	PC3	9.4	*

4. Discussion

4.1. Distribution and habitat use

The otter was widespread in the study area, although positive sites tended to be concentrated at middle elevations, while the species tended to be absent from both high mountain environments and the increasingly dry and salty lowlands. Marking intensity values in our study area did not depart from the general patterns observed for the western Palearctic, based on studies developed under a wide variety of

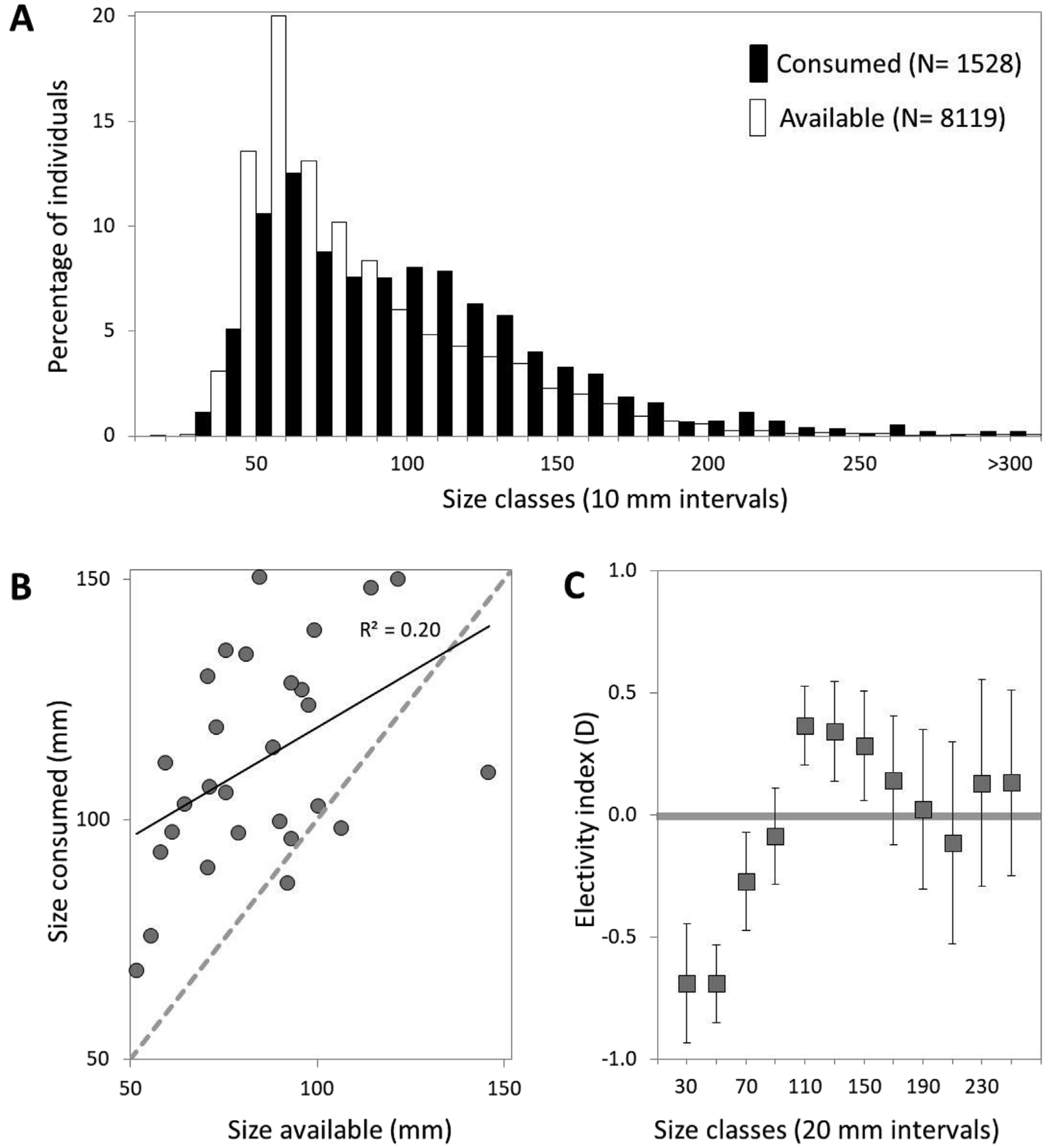

Fig. 5. A: size structure of barbels (*Luciobarbus lepineyi* and *Luciobarbus pallaryi*) consumed by the otter (black columns) and captured during the fish surveys developed in the study area (white columns). B: linear relationship between the average size of barbels consumed by the otter and captured through electrofishing at the same sites. The broken line marks 1:1 relationship (i.e. average sizes of available and consumed fish being equal). C: Selectivity (Ivlev's D index) by the otter of different barbel size classes, with the thick grey line marking no selectivity (i.e. zero D value), separating preferences (positive values) and avoidances (negative ones). Squares are average values for the different sites and whiskers are 95% confidence intervals.

environmental conditions. This suggests that while harsh environmental conditions may limit the distribution of the otter in the studied basins (see below), otter densities in occupied river stretches might not be lower than those reported in wetter environments.

Our results describe an otter distribution pattern that is strikingly similar to that reported by Broyer et al. (1988) for the mid-1980s. Broyer et al. (1988) visited 34 sites in our study area, finding otter signs in 20 (i.e. 59%) of them, almost the same figure reported here (61%). But beyond prevalence, both works coincide in reporting the absence of the otter in right-margin tributaries of the middle Draa, in Oued Rheris and at high elevations, and its ubiquity along the Draa and Ziz main courses. These consistencies suggest that the status of the otter in the country has remained relatively stable in the last decades, as previously reported by Delibes et al. (2012) for other areas in Morocco. It would be very interesting to investigate whether the status of the species is that much stable in Algeria and Tunisia.

Distribution patterns reported here suggest a double limitation for otters in the study area: harsh environmental conditions at high elevations and aridity in the lowlands. This results in a unimodal response of the probability of otter presence across the altitudinal gradient. The species is arguably unable to inhabit high mountain environments due to the lack of sufficient trophic resources (e.g. Remonti et al., 2009), although physiological constraints are also plausible (Crait et al., 2012). We found that otters tend to be absent above 2100 m a.s.l. This pattern was confirmed through an intensive sampling of high-mountain streams of the Draa basin (Clavero et al., 2018), during which no otter signs were found. In the lowlands, below some 800 m a.s.l. in our study area, the limitations to otter presence may be related to the lack of superficial waters and/or to their extreme salinities (Clavero et al., 2015), since otters need low-salinity water to drink and wash their fur (Somers et al., 1998; Beja, 1992). As a result, the otter was absent in the lowest reaches of the Draa and Ziz basins. However, otter distribution in Oued Ghir expands southward from the limits of our study area (i.e. into the Algerian Sahara), reaching at least the Djorf-Torba reservoir (Nait-Larbi, 2011), some 50 km to the south of our lowest site. The lowland extreme of the unimodal relationship between otter distribution and elevation in our arid study area is different from similarly unimodal patterns described in other areas (e.g. Clavero et al., 2010), where otter presence in lowland areas is apparently hindered by human impacts.

Arid conditions can make otter populations more vulnerable to local extinctions and also hinder recolonization processes after extinction events. This might be the case of the Rheris basin, where the otter has been absent at least since the 1980s in spite of the availability of suitable habitats with abundant barbel populations (Clavero et al., 2017 and authors' unpublished data). The otter has not been able to (re)colonize Oued Rheris even though its distance to Oued Ziz its only 3 km south of the town of Erfoud (both water courses then separate from each other, to definitively join some 80 km southwards, to form Oued Saoura). This proximity was artificially created by the diversion of Oued Ziz during the Middle Ages, in order to make it flow by the city of Siǧilmāsa (Capel., 2016). Otter movement between oueds Ziz and Rheris is arguably hampered by the extreme harshness of the terrestrial habitats separating these nearby water courses. In more humid environments the otter has been shown to have a large recolonization capacity, being able to occupy basins from where it had become extinct from neighboring ones by crossing water divides and tens of kilometers of terrestrial habitats (Janssens et al., 2008; Jiménez et al., 2009).

4.2. Diet

We found that otter diet in the area was dominated by fish in general and barbels in particular, with amphibians and reptiles being the only relevant secondary prey. These results are surprisingly coincident with those reported by Broyer et al. (1988) after analyzing 224 spraints from the Draa (11 spraints), Ziz (51) and Guir (162) basins. These authors provided RFO values of 76% for fish (76% in our dataset, see Table 3), 15% for amphibians (18% in our dataset) and 4% for reptiles (also 4% in our data). The RFO of fish in our study area is high if framed in a European context, being clearly larger than the average values reported for the Iberian Peninsula (65%; Clavero et al., 2008), and closer to the figures of temperate European areas (80.6%) than to those of the Mediterranean ones (62.6%) (Clavero et al., 2003). Within the European temperate area, they are closer to the figures of standing waters (~85%) than to those of rivers and streams (slightly over 50%) (Krawczyk et al., 2016). The RFOs of fish are also high in the other available reports of otter diet in Northern Africa (Libois et al., 2015a,b). Amphibian consumption also seems to be high in our study area, since, according to the review by Smiroldo et al. (2019), the RFO of amphibians is rarely higher than 15%. Amphibian consumption increased at higher elevations, as already reported in other areas (Remonti et al., 2009). The lack of large crustaceans in our study area, either crayfish or freshwater crabs, which can be relevant otter prey (e.g. Georgiev and Stoycheva, 2006; Ruiz-Olmo and Clavero, 2008), leaves amphibians as the sole important alternative resource to fish prey. This situation could however change if invasive crayfish already present in Morocco (e.g. Yahkoub et al., 2019) spreads throughout the country.

The predominant role of barbels in otter diet in our study area coincides with the trophic spectrum already reported in rivers of Morocco (Libois et al., 2015b), Algeria (Libois et al., 2015a) and the Iberian Peninsula (e.g. Ruiz-Olmo et al., 2001; Blanco-Garrido et al., 2008). In the studied basins, barbels are the only widely distributed fish, and alternative fish prey are found only at high elevation reaches (trout) or lowlands (tilapias), or linked to reservoirs (non-native species) (Clavero et al., 2017). Consequently, the frequency of barbel consumption described here is amongst the highest recorded for any otter population. Otters generally reject the smallest size classes of available prey fish populations (e.g. Taastrøm and Jacobsen, 1999; Kloskowski et al., 2013; Mirzaei et al., 2010), as is the case for barbels in our study area, although Miranda et al. (2006) reported an Iberian otter population selecting notably smaller barbels, preferring individuals below 80 mm. Barbels predated by otters in our study area are also larger than those reported from the Middle Atlas (Libois et al., 2015b), where 87% of the *Luciobarbus labiosa* consumed by the otter were smaller than 100 cm, this figure being 53% in our dataset. However, larger average sizes of consumed barbels (between 120 and 180 mm) have also been reported for the Iberian Peninsula (JIménez, 2005). The environmental (e.g. flow variability) and biotic (e.g. community composition, invasions) determinants of prey size preference by otters are an interesting research line, attending at the large diversity of patterns reported in the literature.

4.3. Otters in arid lands

The generalized lack of otters in the lowlands of our study area and the particular case of Oued Rheris highlight the vulnerability of the otter in arid environments. This vulnerability is expected to increase in the study area in the next future, due to the expected increases in temperatures and reductions in precipitation (Schilling et al., 2012; Karmaoui et al., 2014). The unsuitable conditions for otter presence in the lowlands reported here are thus expected to move uphill, but this shift will not be compensated by an increase of suitability in mountain areas, due to limitations in water availability (e.g. Clavero et al., 2018). As a result, otter distribution in the area is expected to shrink, increasing the probability of local extinctions and hindering recolonization events. Notably, the observed and projected climatic patterns in the Mediterranean region (Cramer et al., 2018) indicate that aridity may become an increasingly limiting factor for otter distribution and a determinant of its ecology in other areas of Northern Africa and Southern Europe.

CRediT authorship contribution statement

Maria Riesco: Investigation, Investigation, Formal analysis, Writing - original draft. **Miguel Delibes:** Investigation, Writing - review & editing. **Javier Calzada:** Investigation, Writing - review & editing. **Javier Esquivias:** Investigation. **Abdeljebbar Qninba:** Writing - review & editing. **Miguel Clavero:** Investigation, Formal analysis, Writing - original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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