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Research Article

I mark where I eat: a fine scale spatial pattern of the Eurasian otter diet along three rivers in southern Italy

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Abstract

The Eurasian otter *Lutra lutra* suffered a sharp decline in the last century caused by multiple pressures, including human persecution, habitat loss, and water pollution. In Italy, the species is currently listed as Vulnerable in the Italian Red List. For top predators a sound knowledge of the feeding ecology is essential to adopt effective conservation strategies, especially at local scale. We analysed the trophic niche of the Eurasian otter in three rivers located in the core area of the Italian otter range and compared niche width and prey composition among river sectors. Prey remains were examined in 415 spraints collected from July to October 2019 at 17 frequent marking sites along seven river sectors (one upstream, three medium course, and three downstream). Differences in the probability of occurrence of five prey categories (fish, crustaceans, amphibians, reptiles, and insects) were compared among rivers and river sectors through Generalized Linear Mixed Models. Pianka index (O_{jk}) was used to evaluate the trophic niche overlap among rivers sector pairs. Results showed that fish was the main prey in the whole study area, followed by crustaceans, amphibians, insects, and reptiles. However, prey remains in spraints reflected prey composition at very local scale, with fish prevailing in all downstream sectors, while amphibians, crustaceans, and insects mainly represented in the middle sectors. The endemic crayfish *Austropotamobius italicus* was almost the unique prey in the single upstream investigated. Accordingly, trophic niche differed more among river sectors within the same river ($O_{jk} = 0.21-0.28$) than among same sectors (i.e., downstream and middle course) of different rivers ($O_{jk} > 0.6$). This spatial pattern is discussed both in terms of behavioural ecology and digestive physiology of the Eurasian otter.

Introduction

In the past century, several stressors, such as human persecution, habitat degradation, and pollution, led to a severe decline of the Eurasian otter *Lutra lutra* in Europe (Loy et al., 2022). Following law enforcement and the banning of harmful pollutants (Roos et al., 2012; Stockholm Convention, 2001), the species is now recovering in most European countries (Loy et al., 2022), including Italy, where it has been recently downgraded from Endangered to Vulnerable in the national red list (Loy et al., in press; Rondinini et al., 2022). Once widespread in the whole peninsula, in the '90 of the last century the species went extinct in northern and central Italy, and a viable population only survived in southern regions, completely isolated from other European populations (Panzacchi et al., 2011). The ongoing recovering allowed a recent return to central (Loy et al., 2023; Marcelli et al., 2023; Giovacchini et al., 2018, 2023) and northeastern Italy (Stokel et al., 2022; Giovacchini et al., 2021; Lapini et al., 2020; Malthieux, 2020; Marcolin et al., 2020; Pavanello et al., 2015; Righetti, 2011). However, the core otter range is still limited to the south-central portion of the peninsula, still isolated from other European populations (Giovacchini et al., 2021). Moreover, the genetic uniqueness of this population suggests it represents an Evolutionary Significant Unit (Mucci et al., 2010; Randi et al., 2003) in need of specific conservation efforts. Successful conservation efforts of ESU should account for their

local adaptations and ecological requirements. For threatened top predators, it is crucial to thoroughly understand feeding ecology and identify both key feeding resources and prey resources that might expose populations to conflicts with humans or other endangered species (Arrizabalaga-Escudero et al., 2015; Freitas et al., 2007). Otters are opportunistic predators that feed on aquatic and semi-aquatic prey (Roos et al., 2015; Panzacchi et al., 2011; Kruuk, 2006). When available, otters eat almost exclusively fish (Remonti et al., 2007; Fusillo, 2006; Prigioni et al., 1991a,b; Ruiz-Olmo et al., 1989). However, the diet also includes amphibians, crustaceans and, to a lesser extent, small mammals, reptiles, birds, and other invertebrates (Remonti et al., 2007; Fusillo, 2006; Polednik et al., 2004; Clavero et al., 2003; Ruiz-Olmo et al., 2002; Prigioni et al., 1991a,b).

Although the otter diet has been studied in many European countries (Bedmar et al., 2022; Boyi et al., 2022; Dettori et al., 2022; Sittenthaler et al., 2021; Harper et al., 2020) including Italy (Loy et al., 2023; Buglione et al., 2020; Smiroldo et al., 2019b), no authors have yet analysed if and how diet composition varies along the river gradient or among neighbouring rivers. This information is valuable to both infer prey resource exploitation pattern by otters, and to manage prey communities at both local and river basin scales (Arrizabalaga-Escudero et al., 2015). To fill this gap, we analysed the fine-scale spatial pattern of the trophic niche of otters along three neighbouring rivers in the core area of the Italian otter range in Southern Italy.

We specifically examined prey remains in otter scats (spraints) to first characterize otter diet in the study area, and then to answer three main

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questions that could contribute to understanding the spatial pattern of resource exploitation by otters. As community composition (e.g., fish, macroinvertebrates, etc.) is known to vary along the river gradient (Marconato et al., 2002; Huet, 1949) and otters are opportunistic predators (Kruuk, 2006) do prey remain composition change along the river gradient according to the local composition of prey (RQ1)? Does prey composition in spraints vary among different rivers (RQ2)? Does feeding niche overlap across same sectors of different rivers (RQ3)?

Materials and methods

Study area

We investigated the rivers Bussento, Mingardo, and Lambro flowing in the Cilento, Vallo di Diano and Alburni National Park, within the core otter range in southern Italy in the region of Campania (Fig. 1). The Bussento river is 37 km long, with a catchment area of 352 km² and runs across a heterogeneous landscape, including a 5 km sinkhole. The Mingardo river is 38 km long with catchment area of about 230 km², while the Lambro river as a total length of about 24 km and a catchment area of approximately 77 km². The mean annual rainfall is about 998 mm (www.scia.isprambiente.it).

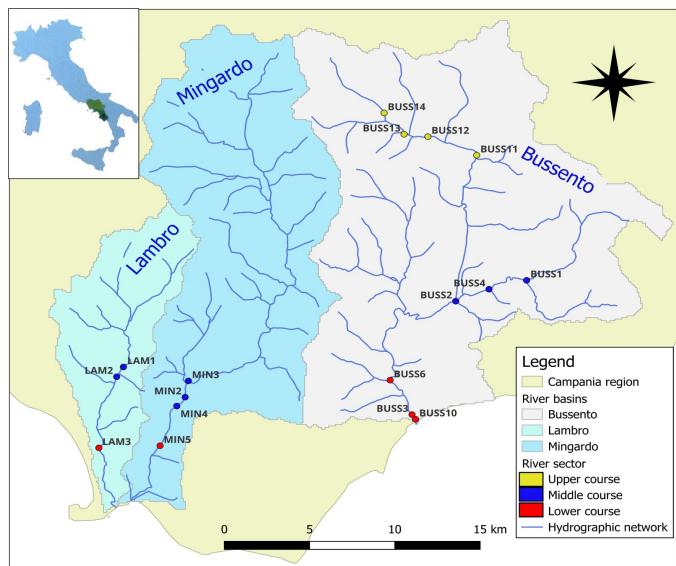


Figure 1 – Sampling sites along the rivers Mingardo, Bussento and Lambro in Campania, Italy. Colors of the sites indicate the different river sectors sampled.

Spraint collection and prey identification

Otter spraints were collected at 17 sampling sites along the main courses of Bussento (n=10, river length: 30 km from the river mouth up to 435 m a.s.l.), Mingardo (n=4, river length: 9 km from the river mouth up to 60 m a.s.l.), and Lambro (n=3, river length: 11 km from the river mouth up to 85 m a.s.l.) (Tab. S1). Sampling sites were selected among frequently marking river stretches. Sampling sites were assigned to the lower (<5 km from the river mouth), middle (5–25 km), and upper (>25 km) course of each river. Accordingly, sampling sites were then assigned to two river sectors (lower and middle course) for Lambro and Mingardo rivers, and three for Bussento river (Fig. 1). Details on specific distances among sampling sites and river sectors are reported in Table S1.

Spraints were collected during five sampling sessions ran in July, September, and October 2019, for a total of 40 sampling days. Spraints were collected by walking along both riversides for 600 m of river stretch (Jawwal et al., 2021; Balestrieri et al., 2011; Reuther et al., 2000). Each spraint was preserved in a paper bag and then soaked in water containing a cleaning capsule of potassium monopersulphate for at least 6 h (Jenkins et al., 1979). Remains were then washed using a 0.5 mm mesh sieve under running water to clean and separate hard parts from the matrix. Hard parts were examined using a bin-

ocular microscope and assigned to the lowest taxonomic level, using identification keys for fish (Gagliardi et al., 2006; Conroy et al., 2005; Dondolin, 1999; Webb, 1976), amphibians (Smiraldo et al., 2019c; Di Palma and Massa, 1981), reptiles (Di Palma and Massa, 1981), birds (?Day, 1966), and mammals (Chaline et al., 1974; Day, 1966). Fish were identified based on hurophore complexes, pharyngeal teeth, opercular and preopercular bones, scales, dentary, maxillary, caudal and thoracic vertebrae, and branchial arches and otholiths. Identification of amphibians was based on femur, tibia-fibula, scapula, ilion, premaxillary and maxillary bones. Exoskeleton remains were used to identify crustaceans (crayfishes and crabs). Exoskeleton, legs, head, and wings remains were used to detect the presence of insects. Hairs, teeth, feathers, and claws revealed the presence of mammals and birds.

Data analysis

Prey remains were assigned to eight prey categories: fish, amphibians, crustaceans, reptiles, insects, molluscs, birds, and mammals. For each prey category we recorded the presence (1) or absence (0) in each spraint (Tab. S2) Prigioni et al. (2009); Remonti et al. (2007). Presence/absence data were first converted into Percentage Frequency of Occurrence (PFO), i.e. the total number of spraints containing a specific prey item by the total number of spraints × 100 (Smiraldo et al., 2019a; Conroy et al., 2005; Webb, 1976). To evaluate the minimum sample size needed to represent the whole prey category assemblage, we computed accumulation curves for the whole study area and for each river sector. All curves showed that the minimum sample size was reached in every river stretch but the upper sector of Bussento (Fig. S4).

Probability of Occurrence (PO) of each prey category was obtained by fitting four General Linear Mixed Models (GLMMs; McCullagh and Nelder 1989) to the presence/absence matrix. A first model (M1) was calibrated to assess PO of prey categories in the whole sample, setting prey presence/absence in each spraint as the response variable (see Tab. S3. for an example of the input matrix), and the prey category as the explanatory variable. The same analysis was applied to other three models, to test the effect on PO of i) prey category, river sector irrespective of river (lower or medium), and their interaction (M2), ii) prey category, river sectors within Bussento river (upper, middle, and lower), and their interactions (M3), prey category, river, and their interaction (M4). Prey categories with PO < 0.1 were not analysed. To account for spatial autocorrelation in model residuals, we set the sampling site as a random effect nested within sector and river (M1), within river (M2 and M3) or within sector (M4). Model goodness-of-fit was assessed through conditional R² (Nakagawa and Schielzeth, 2013), while predictive performance was quantified through a five-fold cross-validation approach, calculating the area under the receiver operating characteristic curve (AUC; Hanley and ?). As a post-hoc test, we performed a pairwise comparison between marginal means (i.e., the difference in fitted means between each river and sector) through ANOVA with F-tests and p-values quantified via the Kenward-Roger's method for denominator degrees-of-freedom and F-statistic. The statistical significance was assessed through Kenward–Roger p-values (Gomez et al., 2005). All the analyses were carried out using “lme4”, “lmerTest” and “performance” R packages (Lüdecke et al., 2021; Kuznetsova et al., 2017; Bates et al., 2015).

The feeding niche overlap among river sector pairs within each river and among lower and medium sectors of the three rivers was evaluated through the Pianka index (Baghli et al., 2002) on PFO values, as follows:

$$O_{jk} = \frac{\sum_i^n (p_{ij} \times p_{ik})}{\sqrt{\sum_i^n p_{ij}^2 \times \sum_i^n p_{ik}^2}}$$

where p_{ij} and p_{ik} indicate PFO in the j sector and k river respectively. Pianka's index ranges from 0 (no overlap) to 1 (total overlap). A Spearman's correlation test was also performed to test the hypothesis of independence between the overlap niche (Pianka index) and the distance between the river sectors. The result ρ can range between -1 to +1. Extreme values indicate maximum correlation, whereas the correlation is null close to 0.

Results

A total of 415 spraints were collected along 17 sampling sites: 188 (45.3 %) in Bussento, 123 (29.7 %) in Mingardo, and 105 (25 %) in Lambro rivers (Tab. S1). Results from model M1 comparing PO of each prey category in the whole sample pooled for the three rivers (Fig. 2) produced a fair predictive performance (AUC=0.75), even though with a relatively low goodness-of-fit (cond. $R^2 = 0.24$). As expected, fish showed the highest average probability (PO=0.67), followed by crustaceans (PO=0.39), amphibians (PO=0.25), insects (PO=0.23), and reptiles (PO=0.11). All pairwise comparisons were significant at $p < 0.001$, with the only exception of the difference between amphibians and insects (Tab. S5). The remaining categories, i.e., mollusks, mammals and birds were the least exploited resources (PO<0.1).

According to PFO, fish were the main prey in the otter diet in five out of seven river sectors. Crustaceans resulted to be almost the unique food item in the upper Bussento sector. Amphibians prevailed as primary trophic source in the middle course of two out of three rivers (Bussento and Lambro). Finally, insects were the first food category in one river sector only (middle course of Lambro) (Tab. 1).

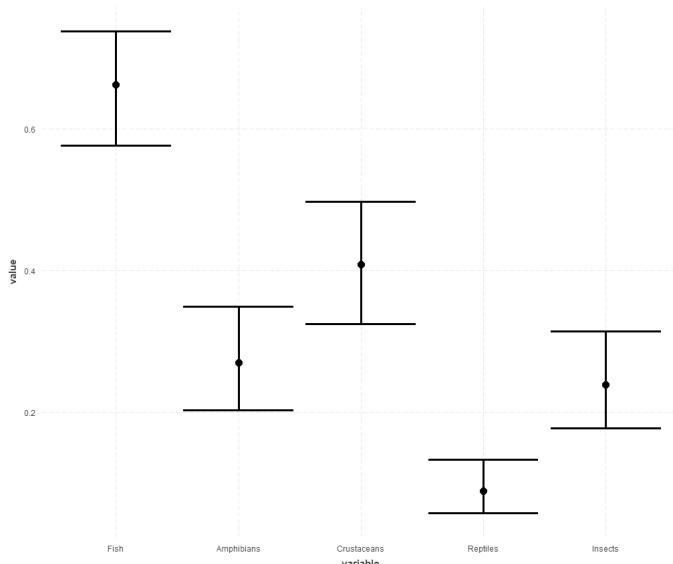


Figure 2 – Box plots showing average probability of occurrence (PO) and standard deviation of each category of prey in the total sample, as modelled by M1. Molluscs, mammals, and birds are not shown (average PO<0.1).

A comparison of otter prey composition between the middle and lower course of the rivers (model M2) confirmed fish as the main prey category in both sectors (Fig. 3). However, the proportion of fish was significantly higher in the lower (PO always >0.6) than in the middle

(PO always <0.6) sector. Conversely, the other prey categories were more represented in the middle than in the lower course (Tab. S6). The model achieved a good predictive accuracy (AUC=0.77) and a goodness-of-fit equal to 0.29 (cond. R^2).

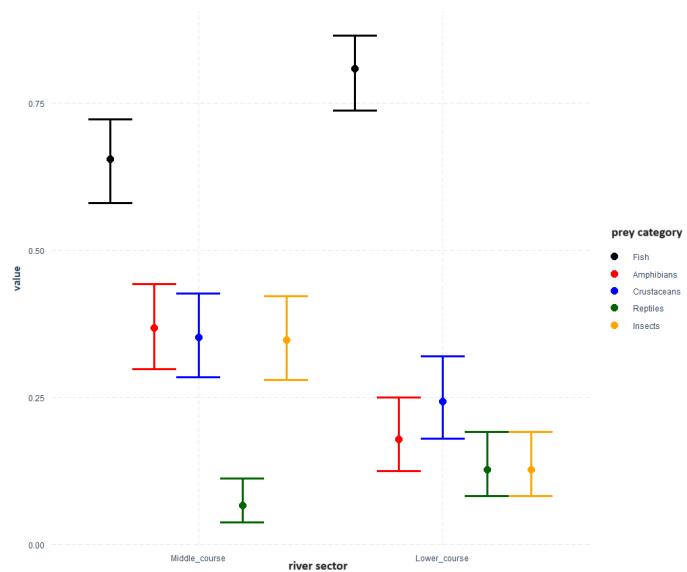


Figure 3 – Box plots of PO of prey categories in middle and lower course sectors of the three rivers, as modelled by M2. Molluscs, mammals, and birds are not shown (PO < 0.1).

Model M3 exploring changes in prey composition along the river gradient of Bussento achieved a good predictive accuracy (AUC=0.808) and a goodness-of-fit slightly higher than M1 and M2 (cond. $R^2=0.39$). Prey composition differed significantly in the upper, middle, and lower sectors of the river (Tab. S7). Specifically, in the upper course, prey remains were almost only represented by crustaceans, mainly belonging to the endemic crayfish *Austropotamobius italicus* (PO close to 1). It should be underlined that according to accumulation curves (Tab. S3) this latter result could be biased by an inadequate sample size to represent other prey categories. However, as PFO of crayfish was 97.9 %, the influence of alternative prey could be considered negligible (Tab. 1). Moving from the upper to the lower course, prey composition shifted from crayfish to mainly fish (Fig. 4). Specifically, fish was the almost exclusive prey item in the lower course (PO>0.75), while the middle course was mainly characterized by fish and amphibians (PO close to 0.75), followed by crustaceans and insects (PO close to 0.5), and reptiles (PO close to 0.10). (Tab. S7).

Finally, when comparing prey categories among rivers (model M4), the model obtained a fair predictive accuracy (AUC=0.78) and a similar fitting value (cond. $R^2=0.35$) compared to M3. Fish were again the most represented prey category in each river, although with some

Table 1 – Percentage of frequency of occurrence (PFO) of prey categories in the whole study area, in each river, in pooled lower and middle sectors, and in each individual sector.

| | Fish | amphibians | crustaceans | reptiles | insects | molluscs | birds | mammals |
|-------------------------------|------|------------|-------------|----------|---------|----------|-------|---------|
| Bussento upper course | 2 | 2 | 97.9 | 2 | 2 | 0 | 0 | 0 |
| Bussento middle course | 72.2 | 72.2 | 27.7 | 5.6 | 44.4 | 5.6 | 0 | 0 |
| Bussento lower course | 72 | 15.5 | 21.3 | 10.7 | 13.1 | 5.7 | 4.1 | 1.6 |
| Mingardo middle course | 100 | 15.9 | 39.3 | 12.7 | 14.9 | 0 | 0 | 2.1 |
| Mingardo lower course | 88 | 25 | 45.8 | 20.8 | 0 | 4.2 | 0 | 0 |
| Lambro middle course | 50 | 50 | 30.6 | 0 | 52.2 | 1.1 | 0 | 0 |
| Lambro lower course | 69 | 18.8 | 37.5 | 6.3 | 25 | 0 | 12.5 | 0 |
| Middle course | 67 | 36 | 34.5 | 6.5 | 33.8 | 1 | 0 | 1 |
| Lower course | 73.5 | 17.2 | 23.3 | 12.3 | 12.3 | 4.9 | 3.1 | 1.2 |
| Bussento river | 88.7 | 23.4 | 22.7 | 9.9 | 17 | 5.7 | 3.5 | 1.4 |
| Mingardo river | 83.0 | 17.8 | 40.6 | 14.4 | 11.8 | 0.9 | 0 | 1.8 |
| Lambro river | 52.9 | 45.1 | 26.9 | 1.9 | 48.7 | 1 | 0 | 0 |
| Overall sample | 62.7 | 25.1 | 38.1 | 8.2 | 22.2 | 2.4 | 1.2 | 1 |

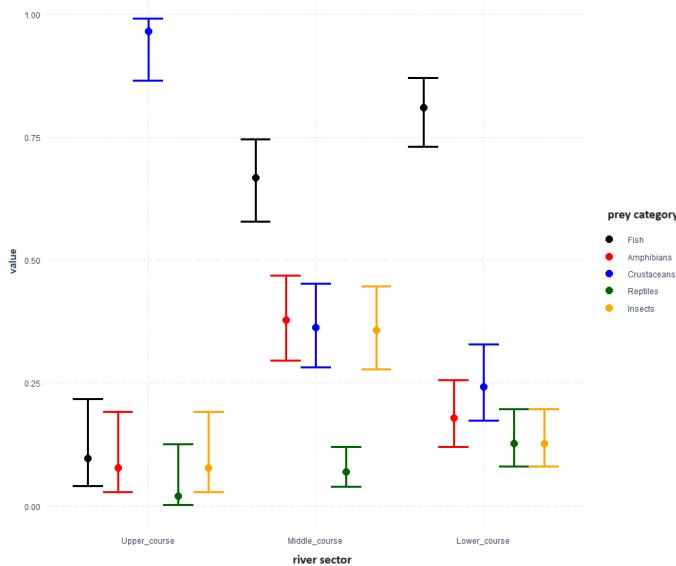


Figure 4 – Box plots of PO of prey categories along different sectors of the Bussento river, as modelled by M3. Molluscs, mammals, and birds are not shown (PO < 0.1).

difference in their prevalence (Fig. 5). Specifically, in the Bussento river fish were significantly higher than all the other prey categories (PO>0.75) (Tab. S6). In the Mingardo river fish (PO>0.75) and crustaceans (PO>0.35) were significantly higher than other categories (Tab. S6). Finally, in Lambro river fish frequency was not significantly higher than amphibians, crustaceans or insects, and only reptiles were significantly lower than all other categories (PO>0.05) (Tab. S8).

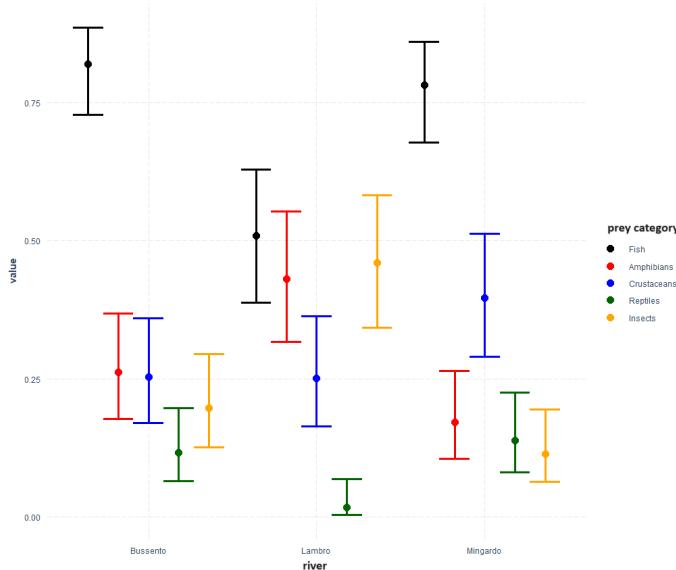


Figure 5 – Box plots showing mean and standard deviation of Probability of Occurrence (PO) of prey categories in the three rivers, obtained by pooling the middle and lower course, as modelled by M4. Molluscs, mammals, and birds are not shown (PO<0.1).

The mean niche overlap index between sector pairs of the same rivers (mean $O_{jk}=0.43$, $SD=0.25$) was lower than the niche overlap between sectors of different rivers (mean $O_{jk}=0.71$, $SD=0.34$). The least overlap was found among the sectors of Bussento river (all values lower than 0.3), whereas Mingardo and Lambro rivers showed a high degree of overlap between the middle and the lower sectors of the river, ranging from 0.68 to 0.72 (Tab. 2). When we explored the overlap index between the same sectors of different rivers, all values were above 0.5, with the highest overlap shown between the middle course of Bussento and Lambro rivers (Tab. 3). Instead, Spearman correlation between overlap indices and distance among sectors was low ($\rho = -0.314$), suggesting that niche similarity was not related to distance between sectors.

Table 2 – Pianka niche overlap index O_{jk} and linear distances between sector pairs of the same river. Distances are measured following the hydrographic network.

| Sector pairs | Distance (km) | |
|--------------------------------------|---------------|------|
| Bussento upper course* middle course | 0.28 | 10.5 |
| Bussento upper course* lower course | 0.21 | 17.5 |
| Bussento middle course* lower course | 0.25 | 7.1 |
| Mingardo middle course* lower course | 0.68 | 3 |
| Lambro middle course* lower course | 0.72 | 6.3 |

Table 3 – Pianka overlap index O_{jk} and linear distances between the same sectors (middle or lower course) of different rivers. Distance between sampling sites of different river basins are linear distances.

| Sector pairs | Distance (km) | |
|--|---------------|------|
| Bussento middle course* Mingardo middle course | 0.61 | 15.7 |
| Bussento middle course* Lambro middle course | 0.93 | 19.5 |
| Mingardo middle course* Lambro middle course | 0.55 | 4.2 |
| Bussento lower course* Mingardo lower course | 0.62 | 15 |
| Bussento lower course* Lambro lower course | 0.66 | 18.6 |
| Mingardo lower course* Lambro lower course | 0.78 | 4.1 |

Discussion

Our study allowed us to detect up to eight categories of prey in the diet of the Eurasian otter in the study area, confirming a broad trophic niche of otters in Mediterranean areas compared to other European biomes (De Sanctis, 2020; Krawczyk et al., 2016; Lanszki et al., 2016; Clavero et al., 2003). As expected, fish was the main prey category in our study area. In fact, it is widely recognized that otters prefer fish and that their demographic parameters are directly influenced by fish abundance (Kruuk, 2006; Ruiz-Olmo et al., 2001). Prey preference tests conducted in captivity always showed fish as the favorite food item (Erlinge, 1968). However, a broader feeding niche observed in Mediterranean otters has been related to fluctuations in the water regime of rivers and water extraction, which are reflected in fluctuations in fish stocks, making alternative prey relevant food resources in specific seasons or areas Rytwinski et al. (2023); Gil-Sánchez and Antorán-Pilar (2020); Remonti et al. (2009); Ruiz-Olmo et al. (2001). More specifically, in Mediterranean areas fish are less consumed, with crayfish and reptiles as main alternative prey De Sanctis (2020); Marcolin et al. (2020); Lanszki et al. (2016); Remonti et al. (2007); Fusillo (2006); Prigioni et al. (1991a,b); Ruiz-Olmo et al. (1989). Our study partially confirms this evidence, as crustaceans were the main alternative prey, but amphibians replaced reptiles as the second main alternative item. Interestingly, both fish and crustaceans' exploitation were significantly higher than other prey categories, whereas reptiles were significantly less likely to occur in the diet. A prevalence of amphibians over reptiles was also observed in other southern Italian rivers by Remonti et al. (2009).

Surprisingly, insects were another locally important food consumed by otters in our study area, especially in the Lambro river, where they represented the second most frequent prey, and the main prey in the middle sector of the river. Insects as alternative prey for otters were observed by Adrian and Delibes (1987) in Donana (Spain) and are known to be actively preyed by otters (Taylor et al., 2010). According to Meakins (1976) and Driver (1981), insects provide a high caloric intake and are particularly easy to catch and ingest (Hansen, 2003; Reid et al., 1994). Thus, predation upon insects is in accordance with the optimal foraging theory (Pyke and Starr, 2021). However, as amphibians and insects were represented almost equally in all river sections, the latter could represent the undigested prey of amphibians rather than being directly preyed on by otters, as suggested by other authors (Remonti et al., 2007; Hansen, 2003; Larsen, 1984; Toweill, 1974).

Focusing on otter diet along the river gradient, our results showed that fish were more abundant in the otter diet in lower sections of all rivers, whereas amphibians and insects were more represented in the

medium sections, and crustaceans were the exclusive prey in the upstream section. A similar shift in otter diet along the river has been observed also by Macarthur (2022). Also, electrofishing campaigns conducted along the same rivers showed a high fish density in the lower sectors, whereas in the upper Bussento, native crayfish was the unique freshwater species (Guida et al., 2019; Bianco et al., 2011; Marconato et al., 2002). Moreover, a survey on amphibian conducted in the same rivers revealed an altitudinal gradient of species linked to running waters (i.e. *Rana italica*, *Pelophylax kl. hispanicus*, *Bufo bufo*, and *Hyla intermedia*), with increasing abundances from the mouth of the rivers upward (Romano, 2014). As otters are opportunistic feeders, the prevalence of fish in their diet observed in lower river sections reflects their higher availability in this part of the river, as already suggested by Dettori et al. (2022). In fact, fish composition and abundance are known to vary along the river gradient (Sutela et al., 2020; Huet, 1949). Specifically, fish distribution along rivers responds to the River Continuum Concept that depicts a downstream gradient of organisms following the accumulation of nutrients downward (Welcomme, 1985; Vannote et al., 1980) and leads to a general increase in fish diversity and biomass in the lower stretches of the rivers (Muneepeerakul et al., 2008; Matthews, 1998; Zamora Hernández et al., 1996). Otter capability to include amphibian prey according to their increase in abundance with the altitude is witnessed by our data in middle river sectors (Remonti et al., 2009). Moreover, amphibians are known to typically follow a seasonal trend in otter diet, being more exploited during summer, a season that corresponds to our sampling period (Bauer-Haáz et al., 2014). Finally, in the upper stream section of the river Bussento, fish and amphibians disappeared from the otter diet, as otters fed exclusively on the endemic endangered river crayfish *Austropotamobius italicus*. Based on local surveys conducted in the study area, it has been found that crayfish are only found in this particular section of the river. Additionally, they are the only prey present in this part of the headwater. This region is physically separated from the downstream river sections by a 5 km stretch that runs into a sinkhole. This physical separation is believed to prevent fish recolonization (Bianco et al., 2011; Marconato et al., 2002). Preference tests on food items showed crayfish is the least preferred prey by otters (Erlinge, 1968), evidence also confirmed by Melero et al. (2008) in Spain. This supports the idea of otter feeding opportunistic behaviour as no other prey were available in the upper stretch of Bussento river. Nevertheless, besides being just a secondary prey where fish biomass is scarce (Remonti et al., 2007; Polednik et al., 2004), crayfish seem to be selected by otters when massively present, as they are very easy to catch ?. Otters direct their predation to slower prey (Erlinge, 1968) and switch their diet from fish to crayfish when or where the latter are abundant (Route and Peterson, 1988; Dettori et al., 2021). Abundance of slow-moving prey may have led to a local preference for crayfish over amphibians in the upper Bussento river. To respond to our question RQ1, this evidence suggests that prey remains in otter spraints do change along the river gradient and reflect the local abundance and composition of prey. This hypothesis is also supported by Remonti et al. (2009), who suggested fish reduction at high elevations as the main factor in shaping otter diet at the local scale.

When comparing different rivers, we revealed that fish communities were more exploited in the lower and medium sectors of the Bussento river compared to Mingardo and Lambro rivers. Bussento, Mingardo and Lambro rivers are adjoining river catchments with descending order flow rates. As fish communities are affected by flow rates (Rytwinski et al., 2023; Baran et al., 1995), different river bodies having different flow rates may lead to different carrying capacities for fish. Accordingly, larger rivers like the Bussento river can support higher fish productivity. Moreover, the Bussento river has a more stationary regime due to the hydropower dam located upstream that regulates water release, prevent river drought, and buffers the flow rate during the summer period guaranteeing appropriate habitats for strictly aquatic species like fish (Bovolin et al., 2017). Therefore, higher selection of secondary prey in the Mingardo and Lambro rivers could be related to their lower river flow, which favors availability of alternative prey, as also suggested by Amhaouch et al. (2020). Consumption of amphibians

and crustaceans as alternative feeding resources can also represent a seasonal shift in prey abundance, as our study has been carried out during the dry summer season, when high temperatures and water drought might limit fish abundance and favour alternative prey like crustaceans and amphibians (Prenda et al., 2001). This evidence supports the hypothesis that the otter trophic niche changes among rivers (question RQ2) but also that a similar pattern along every river gradient can also be observed (question RQ3). These outcomes were confirmed by Pianka indices of niche overlap, which evidenced that prey composition differed more along a river gradient than among different rivers. Otter prey remains thus reflect prey community at the very local scale.

Possible explanations of this spatial pattern arise from movement ecology and digestive physiology of otters. Even if occasional long-distance movements are possible, core areas within home ranges are restricted to few kilometres along the river (Lerone et al., 2022; Quaglietta et al., 2019, 2013; Durbin, 1996; Kruuk, 1995). Usually, the core area of an individual otter is around 2–5 km (Quaglietta et al., 2019; Kruuk, 2006; Mason and Macdonald, 1986; Green et al., 1984), corresponding to the average length of river sectors analysed in this study. Moreover, in Mediterranean habitats otters shrink their activities around few remaining feeding sites during the dry season, as well as during freezing winters in northern Europe (Saavedra, 2002; Erlinge, 1967). Accordingly, we hypothesize that river sectors correspond to areas that are exploited intensively before moving to other unexploited portions of the home range (Mitchell and Powell, 2012; Spencer, 1992, 2012), and may corresponds to the daily core feeding areas of 3.5 km of river explored by individuals in a single night reported by Quaglietta (2011) in Portugal. During this hunting activities otters move quiet slowly along the river, with a net displacement of a couple of hundred meters every hour (Quaglietta, 2011).

Additionally, otters have high metabolic rates due to their elongated body shape associated with a remarkable heat dispersion during immersions (McNab, 2008; Iversen, 1972). This, together with the short colon trait, leads to a fast transit time of food during the digestion process (Sá et al., 2014). Time digestion can also vary with activity levels, food caloric contents, and digestive physiology (McGrosky et al., 2016; Carss et al., 1998; Markussen, 1993). Carss et al. (1998) reported an average time of otter digestion of about an hour during active patrolling and hunting.

Accounting for slow movements and short digestion time, the strict relation between prey composition in otter spraints and local feeding resources accurately depict otter diet at fine spatial scale. Effective conservation measures on freshwater top predators should be addressed to also protect prey ecological needs rather than only focusing on the single target species. It is the case of the rare and endemic crayfish *Austropotamobius pallipes* (Chiesa et al., 2010; Brusconi et al., 2008), that in our study area was the exclusive prey in the upstream sector of the Bussento river. These strategies are common for carnivores as they typically are elected as umbrella species, whose protection implies the protection of the whole trophic network (Roberge and Angelstam, 2004). In this sense, it should be paid particular attention to conservation priority issues related to endangered species that are linked by prey-predator relationships, especially if they are jeopardized with few little remnant populations (Fedriani et al., 2017). A proper understanding of how feeding requirements differ in different areas of a river can guide conservation efforts and river management strategies aimed at safeguarding specific components of the river community, particularly those that are restricted to limited areas. In general, our findings confirmed the opportunistic feeding behaviour of the otter in southern Italy and highlighted the diversity of prey offered by the different parts of rivers as a key factor for otter ecological plasticity in the highly Italian human modified landscapes (Loy et al., 2022). ☺

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Table S1 Number of spraints collected.

Table S2 Occurrences of prey categories in the study area.

Table S3 Matrix with the first four observations of each category.

Figure S4 Accumulation curves.

Table S5 Significant pairwise comparisons (model M1).

Table S6 Significant pairwise comparisons (model M2).

Table S7 Significant pairwise comparisons (model M3).

Table S8 Significant pairwise comparisons (model M4).