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RESEARCH ARTICLE

Optimal foraging of Neotropical otters (Carnivora: Mustelidae) in an urban river and predominance of generalist and sedentary fish in their diet

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ABSTRACT. *Lontra longicaudis* Olfers, 1818 is a semi-aquatic carnivore widely distributed in the Neotropical region. Understanding their diet contributes to an indirect understanding of their ecology and the composition of the local fauna. To this end, we analyzed 109 fecal samples and identified 238 morphological structures; these samples were collected between May 2006 and September 2007 from the Santa Lúcia Biological Station (SLBS) in southeastern Brazil. The area is intersected by the Timbuí River, which arrives at the site after crossing the urban perimeter of the city of Santa Teresa in the state of Espírito Santo. We found a predominance of fish in the otters' diets (82%), mainly cichlids (50%), which are fish with sedentary habits and low mobility levels. The crustacean *Trichodactylus fluviatilis* Latreille, 1828 was the third most consumed taxon; this occurred mainly during the rainy season, corresponding to the crustacean's reproductive period, when it is more vulnerable to predation. Otters exhibited a seasonal variation in their prey selectivity. Furthermore, they displayed opportunistic foraging behavior, as the most preyed fish were those with both low mobility and a high frequency in the environment, followed by fish with high mobility and high frequency, and then those with low mobility and low frequency. We concluded that the feeding habits of the otters in the SLBS are in line with the optimal foraging theory since prey selection was optimized through the balance between net energy gained and the energy costs of foraging.

KEY WORDS. Anthropogenic pressure, ecology, opportunism, prey, trophic relationship.

INTRODUCTION

Lontra longicaudis Olfers, 1818, known as the Neotropical otter, is a medium-sized, semiaquatic mammal, usually found along the edges of lakes, rivers, and streams and occasionally in estuaries and mangroves of the Neotropical region (Pardini and Trajano 1999, Uchoa et al. 2004, Rheingantz and Trinca 2015). The species is also present in human constructions like wharves and concrete slabs (Louzada-Silva et al. 2003). *Lontra longicaudis* is currently categorized as 'vulnerable' in the most recent List of Threatened Species for the state of Espírito Santo, Brazil (Costa et al. 2019). The main threats faced by the Neotropical otter are associated with direct and indirect anthropogenic pressure, for instance, hunting and roadkill, and degradation of water bodies and riparian areas, mainly since 2012 due to changes in the Brazilian Forest Code (Rodrigues et al. 2013, Brasil 2010).

Studies on the ecological aspects of Neotropical otters are usually conducted indirectly, through the analysis of the distribution and composition of their feces; these are collected in prominent places in the environments they inhabit, such as on rocks and aquatic vegetation (Uchoa et al. 2004, Rheingantz et al. 2012). These studies have shown that the otters feed preferentially on fish and crustaceans and occasionally on mollusks, mammals, birds, and reptiles (Pardini 1998, Quadros and Monteiro-Filho 2001, Kasper et al. 2008, Carvalho-Junior et al. 2010a, 2010b, Rheingantz et al. 2011). Although the otters' diet is widely studied and known, food composition differs between areas according to the variety and prey abundance. Therefore, understanding the composition of their diet is an indirect approach to unraveling the local ichthyofaunal diversity. Environments under anthropogenic interference are home to fish species with high levels of environmental tolerance (Casatti et al. 2009), which may indirectly indicate an anthropogenic impact on the local biodiversity and indirectly on the otters' habits (Rodrigues et al. 2013).

In this context, the present study aimed to understand the trophic relationship of the otters along a section of the Timbuí River, based on the ecological characteristics of the prey species that are consumed by these animals in the Santa Lúcia Biological Station (SLBS). For this purpose, we used an indirect method to analyze the otters' diet composition.

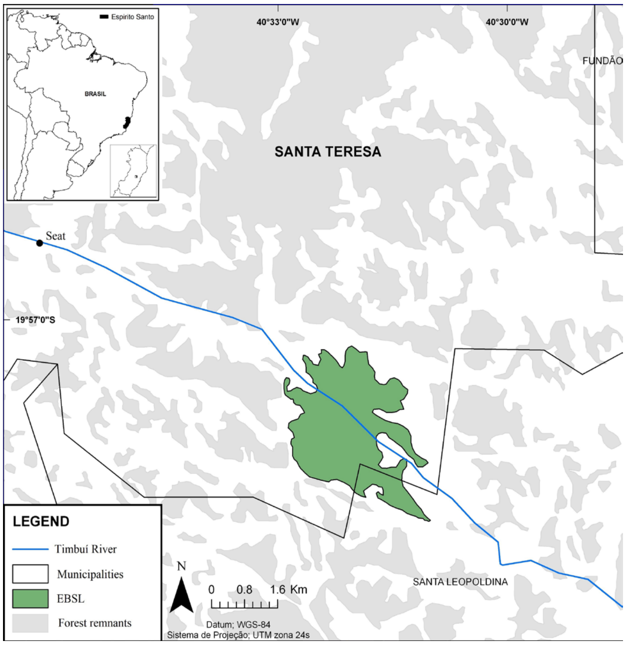

Figure 1. Santa Lúcia Biological Station (SLBS) in the green area. The highlight (blue line) represents the Timbuí river which crosses the municipal seat of Santa Teresa, Espírito Santo, Brazil.

MATERIAL AND METHODS

Study area

The present study was performed along the river banks of the Timbuí, which crosses the SLBS (Fig. 1); the station is a protected natural area of 440 ha located in the municipality of Santa Teresa, in the mountainous region of Espírito Santo, Brazil. The Timbuí River crosses the entire urban perimeter, covering about 8 km until reaching the SLBS, from the northwest to the southeast, in a deep valley, with alternating sections of low inclination and others with rapids or waterfalls (Mendes and Padovan 2000).

The presence of otters in Santa Teresa was detected through direct observations in the field, specimens deposited in collections, and fecal samples, mainly in and from the SLBS, a forest remnant intersected by the Timbuí River. The river crosses the municipal seat before reaching the SLBS, where it receives urban effluents, agricultural waste, and garbage (Mendes and Padovan 2000, Sarmento-Soares and Martins-Pinheiro 2010). A survey conducted between 1997 and 1998 in the SLBS recorded 13 species in the area, in addition to the exotic *Coptodon rendalli* (Boulenger, 1897) (tilapia), *Cyprinus carpio* Linnaeus, 1758 (carp), and *Clarias* sp. (African catfish) (Bernabé 2003), suggesting a low level of local diversity. Although this may be regarded as an early study, given the lack of published information on the ichthyofauna of the Timbuí River, this information is valid if employed with caution.

Sampling

A total of 109 fecal samples were collected during the 17 visits carried out monthly between May 2006 and September 2007. Sampling was performed along an 860-meter-long stretch of the Timbuí's right riverbank in the direction of the river's current, as this is the most accessible stretch. Odoriferous marks and fecal samples of *L. longicaudis* were found in accessible locations of the habitat, such as exposed rocks on the banks and in the riverbed (Fig. 2). Most of the assessed river bank was characterized by a rocky environment with currents and bordered by rocks and arboreal vegetation (Fig. 2A), in addition to sandbanks covered by vegetation in some parts (Fig. 2B).

The collected samples were stored in plastic bags, which were labeled with information regarding the collection date and location. The samples were placed on fine-mesh sieves in the laboratory and washed in running water. They were dried in the open air and in a kiln. The resulting material from the dry samples (fish scales, arthropod exoske-

Figure 2. Stretches of the Timbuí River in the Santa Lúcia Biological Station (SLBS) with environments conducive to the presence of otters: (A) rocky environments; (B) sandbanks covered by vegetation. Images captured on May 27, 2007.

letons, teeth, bristles, nails, bones, and other non-digestible parts) was then sorted. For the comparative analysis of the structures found in otter feces, fish from the zoological collection of the National Institute of the Atlantic Forest from the Timbuí River were dissected to determine the species observed in the feces and to compare them with those recorded in Bernabé (2003). Bones, scales, teeth, otoliths, and other structures were extracted from these specimens; in doing so, we sought to create a reference collection to be used in comparisons with the items found in the feces. Fecal matter and the reference material were compared using a binocular stereoscopic microscope with LED lighting and a magnification of 20 to 40 times.

Data on local rainfall during the collection period (2006 and 2007) were retrieved from the National Institute of Meteorology (InMet 2022) to assess the influence of seasonality on sampling since many rocks covered by rising river levels and feces were washed away by rain during the rainy season. Monthly rainfall averages were compared for dry (February to August) and rainy (September to January) seasons using the Mann-Whitney U test with $\alpha = 5\%$ to determine the seasonality period during sampling. The samples of Bernarde (2003) were on a monthly basis; therefore, our results were adjusted to the same seasons utilized here so that results between that study and ours could be compared.

Data analysis

The Coleman rarefaction curve (Colwell 2013) was obtained using EstimateS9 to certify that the number of samples collected in the study was sufficient to represent the richness of species potentially constituting the otters' diet. The frequency of food items consumed by otters, expressed as a percentage value (%), was calculated by absolute frequency (AF = number of occurrences of each item in the samples x 100/total number of samples) and the relative frequency (RF = number of occurrence of each item x 100/total number of occurrences).

The trend of seasonal variation in the consumption of some diet components was assessed for 17 months; such variation was classified under two categories (wet and dry seasons) based on the analysis of the significant differences in the mean rainfall estimated by the Mann-Whitney U test.

The differences between the AF of each prey throughout the seasons were analyzed using the Mann-Whitney U test for pairwise comparison of samples (Snedecor and Cochran 1980). Our results on the fish consumption of the Neotropical otters, confirmed after the dissections as described above, were compared with the inventory of local ichthyofauna performed by Bernabé (2003). It is important to highlight that Bernabé (2003)'s study was carried out approximately eight years before the sampling of feces took place in the SLBS. Therefore, comparisons must be considered with reservation, as the biota may have been altered during this period.

We tested the null hypothesis of food selectivity (≈ "preference") for fish species using the Ivlev's selectivity index (Wootton 1998), based on a study on the ecology of local fish carried out between 1997 and 1998 by Bernabé (2003): $E = (ri - Pi) / (ri + Pi)$, where: E = selectivity index; ri = percentage of each item in the stomach contents; Pi = percentage of each item in the environment (see Bernabé 2003).

The index values range from -1 to +1; values equal to zero indicate null selectivity, results that are <0 indicate an item's low selection, and >0 stand for a positive selection (Zavala-Camin 1996). Calculations of ri and pi were performed using the frequency of points (FO) method, obtained through the quotient between the number of times a certain item was found in each sample and the total number of items collected (Hynes 1950).

Furthermore, we evaluated the ecological features of the species consumed by the otters in the SLBS in relation to their ease of capture. For this, we considered prey mobility and place of occurrence within the aquatic substrate (Rheingantz et al. 2012).

RESULTS

Otters' diet in SLBS

Of the 109 fecal samples analyzed, 80 were collected during the dry season and 29 during the rainy season. The Coleman rarefaction curve demonstrated a tendency toward stability after approximately 70 samples were analyzed (Fig. 3), which means that the number of samples analyzed was sufficient to establish the richness of the species present in the otters' diet at SLBS. We recorded 238 identifiable morphological structures in the fecal samples collected; these structures belonged to 13 taxa, including fish, amphibians, reptiles, birds, and arthropods.

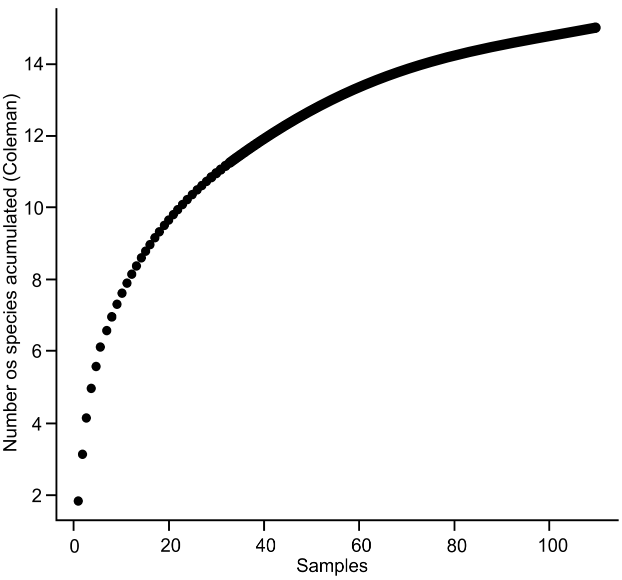

Figure 3. Randomized species accumulation curve (Coleman) for fecal samples of *Lontra longicaudis* collected during the wet and dry seasons in the Santa Lúcia Biological Station (SLBS) between May 2006 and September 2007.

Fish were the main components in the diet of Neotropical otters at SLBS and were present in about 82% of the samples (Table 1). Of the most consumed fish, Cichlidae represented about 50% RF (Table 1), with the pearl cichlid *Geophagus brasiliensis* (Quoy & Gaimard, 1824) as the most consumed fish species (AF=74%; RF=34.03%).

Other fish consumed in frequency order were the exotic species tilapia *Coptodon rendalli* (AF=32%; RF=14.71%), mandi (PTBR) *Pimelodella* spp. (AF=23.85%; RF=10.92%), lambari (PTBR) *Astyanax* sp. (AF=22.01%, RF=10.08%), and wolf fish *Hoplias malabaricus* (Bloch, 1794) (AF=14.67%, RF=6.72%).

The other fish had a low frequency of consumption; these included *Rhamdia quelen* (Quoy & Gaimard, 1824) (jundiá [PTBR], AF=3.66%, RF=1.68%), *Clarias gariepinus* (Burchell, 1822) (African catfish, AF=1.83%, RF=0.84%), *Hypostomus affinis* (Steindachner, 1877) (cascudo [PTBR] AF=0.91%, RF=0.42%), and *Hypomasticus copelandii* (Steindachner, 1875) (piau [PTBR], AF=0.91%, RF=0.42%).

The third most widely consumed component by otters in the SLBS was the freshwater crab *Trichodactylus fluviatilis* Latreille, 1828 (AF=27.52%, RF=12.61%).

Prey selectivity and seasonality

Rainfall data suggest the occurrence of two seasons between 2006 and 2007: a dry season with an average rainfall of 82.4 mm (±33.96) between February and August and a wet season with an average rainfall of 167.2 mm (±83.34) between September and January; the seasons were significantly different according to the Mann-Whitney U test (U = 3; p = 0.018).

Figure 4 depict the results concerning food selectivity. Corresponding to the results of the Ivlev's selectivity index for the dataset resulting from all of the studied months and, the wet and dry periods.

DISCUSSION

Prey characteristics, food selectivity, and seasonality

Fish accounted for more than 80% of the diet composition of otters in the Timbuí River of SLBS. These findings are in line with most studies on the feeding ecology of otters, which also recorded fish as the most consumed taxa, as is the case in the Reserva Biológica Duas Bocas in Cariacica, Espírito Santo (Andrade and Helder-José 1997); Betari River in the upper portion of Ribeira do Iguape, state of São Pau-

Table 1. Absolute frequency (AF) and relative frequency (RF) percentages of the 238 morphological structures consumed by Neotropical otters in the SLBS and present in 109 fecal samples in the municipality of Santa Teresa, Espírito Santo, southeastern Brazil, sampled between May 2006 and September 2007. The updated database of Fricke et al. (2022) was used to name the species. Ecological characteristics of fish families were obtained from Rheingantz et al. (2012), except for Erythrinidae (Oyakawa et al. 2003), Clariidae (Mili and Teixeira 2006), and Anostomidae (Balassa et al. 2004).

Taxon	Popular name	Ecological features	Abundance in the Timbuí River*	N	AF (%)	RF (%)
Ostariophysi						
Cichlidae						
Geophagus brasiliensis	pearl cichlid	Low mobility, pelagic occurrence in aquatic macrophytes	Biomass (1st) Abundance (2nd)	81	74.31	34.03
Coptodon rendalli (exotic)	Tilapia	Low mobility, pelagic in the water column	Visualized but not captured	35	32.11	14.71
Characidae						
Astyanax sp.	Piaba, lambari (PTBR**)	High mobility, pelagic in the water column	Biomass (3rd) Abundance (1st)	24	22.01	10.08
Oligosarcus acutirostris	Piaba-cachorro (PTBR**)	High mobility, pelagic in the water column	Biomass (11th) Abundance (10th)	2	1.83	0.84
Heptapteridae						
Pimelodella sp.	Mandi-chorão (PTBR**)	Low mobility, benthic	Biomass (4th) Abundance (3rd)	26	23.85	10.92
Rhamdia quelen	Jundia (PTBR**)	Low mobility, benthic	Biomass (5th) Abundance (4th)	4	3.66	1.68
Erythrinidae						
Hoplias malabaricus	wolf fish	Low mobility, benthic	Biomass (2nd) Abundance (8th)	16	14.67	6.72
Clariidae						
Clarias gariepinus (exotic)	African-catfish	Low mobility, lentic environment, benthic	Visualized but not captured	2	1.83	0.84
Loricariidae						
Hypostomus affinis	Cascudo (PTBR**)	Low mobility, benthic	Biomass (8th) Abundance (7th)	1	0.91	0.42
Anostomidae						
Leporinus copelandii	Piau (PTBR**)	High mobility, lotic environment, benthopelagic, rheophilic	Not captured	1	0.91	0.42
Amphibians	Frog, toad	–	–	3	2.75	1.26
Reptiles (Ophidia)	Snake	–	–	2	1.83	0,84
Birds		–	–	5	4.58	2.11
Crustacea (Trichodactylidae)						
Trichodactylus fluviatilis	Crab	Low mobility in the rainy season (reproductive)	No information	30	27.52	12.61
Unidentified Insecta				6	5.5	2.52

* According to Bernabe (2003). **PTBR: Brazilian Portuguese (language).

lo (Pardini 1998); Saí-Mirim River in Itapoá, state of Santa Catarina (Quadros and Monteiro-Filho 2001); Mambucada River in Angra dos Reis, state of Rio de Janeiro (Rheingantz et al. 2011); Arroio Grande River in the municipalities of Piratini, São Gonçalo, and Mangueira, state of Rio Grande do Sul (Souza et al. 2013), among others.

Fish of the family Cichlidae, which accounted for about 50% of the otters' diet in the SLBS, have sedentary habits and a limited mobility capacity. They are often restricted to lake shores, near rocks, and aquatic macrophytes (Carvalho-Junior et al. 2010b, Rheingantz et al. 2012), sites that are frequently foraged by these mammals. In the Ribeirão das Lajes reservoir, Gomes et al. (2008) observed the prevalence of otters consuming Cichlidae species, particularly *C. rendalli*, *Cichla ocellaris* Bloch & Schneider, 1801, and *G. brasiliensis*, with relative abundance levels of 50, 18, and 17%, respectively (Agostinho et al. 2007). Prey behavior seems to influence its consumption, with low-mobility fish species more frequent in the otters' diet (Passamani and Camargo 1995, Rheingantz et al. 2012). In addition, these fish can be found in groups in the environment (Andrade and Helder-José 1997), which would ultimately facilitate their capture. Species of *Geophagus*, which was the most consumed fish by otters in the SLBS, are categorized as sedentary (Carvalho-Junior et al. 2010b, Rheingantz et al. 2012). Because it is a low-mobility species (Kullander 2003, Mendes et al. 2021), the significant presence of *G. brasiliensis* in the otters' diet may be attributed to the low energetic cost with which this fish can be captured.

Coptodon rendalli, the second most consumed species by otters in the present study, is very tolerant to wide environmental variations (Avella et al. 1993), has high fecundity and reproductive success (Duponchelle et al. 1998), rapid growth rates (Liti et al. 2005), and an omnivorous habit (El-Sayed 1999). These characteristics contribute to its success in degraded environments and/or as an invasive alien species, generally dominant where it is introduced.

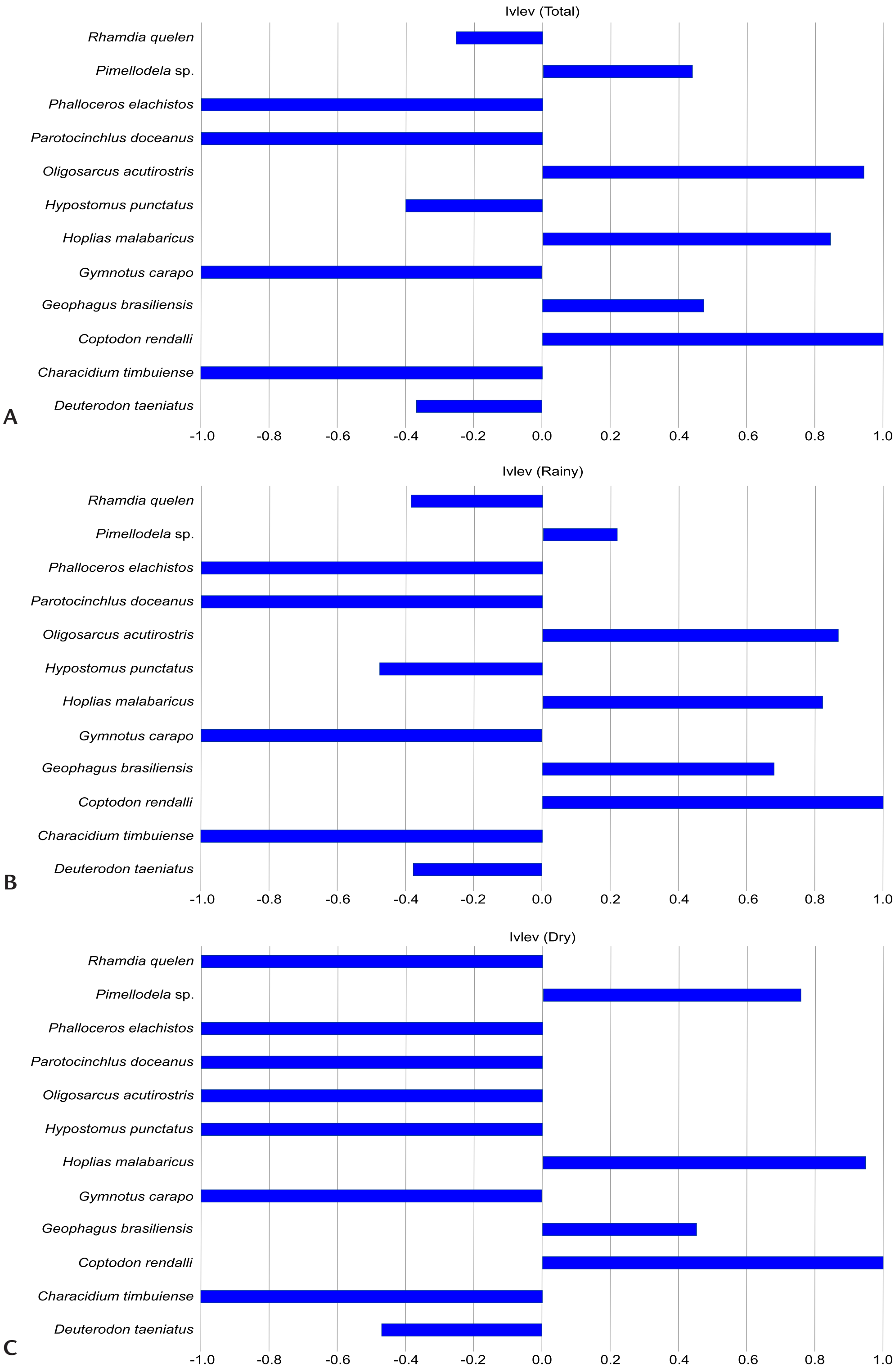

Figure 4. Results of the Ivlev's selectivity index for the dataset from: (A) May 2006 to September 2007; (B) September 2006 to January 2007 (wet season); (C) February to August 2007 (dry season).

We also found two species of Heptapteridae in the otters' diet, although with different frequencies. *Pimelodella* spp. (mandi) was the third most consumed fish species, while *R. quelen* was not very significant in the diet (AF = 3.66%; RF = 1.68%; Table 1). Despite belonging to the same family, these fish have different sizes and behaviors. Whereas *Pimelodella* sp. is smaller, slower, usually occurs in groups, and prefers specific locations and slower waters (Bockmann and Guazzelli 2003, Rheingantz et al. 2012), *R. quelen* is larger, more agile, solitary, and is widespread throughout the aquatic environment (Schulz and Leuchtenberger 2006).

Astyanax sp. (lambari [PTBR]; AF = 22.01%, RF = 10.08%) was the fourth fish and fifth most consumed item by otters in the SLBS. This species is a highly agile characid in the water column (Mili and Teixeira 2006, Rheingantz et al. 2012), and, therefore, its significant consumption cannot be explained by a behavior that could facilitate its capture. *Astyanax* spp., like many Ostariophysi species, have alarm reaction behavior, thus hampering their capture (Pfeiffer 1977, Duboc 2007). One plausible explanation for this finding is that lambaris tend to be very common and abundant in Neotropical rivers (Lima et al. 2003, Pasa et al. 2019), besides having the habit of forming shoals; therefore, their high consumption by the otters could be attributed to their abundance in the area. However, Rheingantz et al. (2012) found that species of Characidae, including those that were abundant but highly agile, were rarely consumed by otters in Angra dos Reis, Rio de Janeiro.

Hoplias malabaricus (wolf fish) was the fifth most consumed fish and the sixth most consumed item in the otters' diet in the SLBS. Species of the Erythrinidae are slow and sedentary (Rheingantz et al. 2012), and wolf fish are considered top predators, ambushing and capturing their prey during the day and at night (Shibatta et al. 2002). *Hoplias malabaricus* is the only erythrinid widely distributed and relatively common in rivers throughout the Neotropics (Oyakawa 2003). The species' behavior and its recurrent presence in freshwater may explain its consumption by otters in the SLBS.

Considering the five fish taxa most consumed by the otters during our sampling in relation to the findings of Bernabé (2003) on fish diversity, abundance, and biomass in the SLBS, we observed that: I) *Geophagus brasiliensis* had the highest biomass and was the second most abundant item in the area between 1997 and 1998; it was also the most consumed item by otters in the diet analysis between 2006 and 2007; II) *Pimelodella* sp. was the species with the fourth-highest biomass and the third most abundant in the river; it was the third most frequent fish in the otters' diet; III) *Astyanax* sp., the species with the third-largest biomass and the greatest abundance, was the fourth most consumed species; IV) *Hoplias malabaricus* placed second among the species with the highest biomass, and it was the eighth-most abundant species and the fifth-most consumed item by the otters; V) *Coptodon rendalli*, the second most consumed species by otters, was not captured by Bernabé (2003). However, the study by Bernabé (2003) was carried out between 1997 and 1998, approximately eight years before our sampling; thus, this level of extrapolation should be carefully evaluated, including the possible fact that its introduction was started only after this period.

Rheingantz et al. (2012) found that very fast fish, even those that are highly abundant in the environment, were seldom consumed by the otters, while sedentary and slow fish, including those less common in the environment, were highly preferred. Therefore, according to the authors, fish abundant along the river stretch, like characids, were the most avoided due to their high velocity. This could explain the low consumption of *Oligosarcus acutirostris* Menezes, 1987 (piaba-cachorro [PTBR]), which is a characid present in the water column and was a rare item in the otters' diet in our study.

Despite being slow and having sedentary habits (Rheingantz et al. 2012), the loricariid *H. affinis* is a benthic animal, occurring predominantly in the lower portion of the river stratum, which may have hindered the otters' access to it. However, Rheingantz et al. (2012) detected longitudinal differences in prey abundance: they recorded the same prey species avoided in one stretch and then preferred in another, possibly due to their relative mobility according to the local waterway characteristics.

Regarding the consumption of species that lack agility, such as the tilapia *C. rendalli* (second most consumed fish), its representativeness in the otters' diet may result from their hunting strategy, which seeks to balance the benefit of capturing the prey with the energetic cost of the endeavor (Pianka 2011, Carvalho-Junior 2007), thus making its foraging more efficient.

The lvlev's selectivity index data showed that otters display a clear preference for five fish species among the 12 analyzed and that the remaining seven were avoided. However, the selectivity varied between the wet and dry seasons: *O. acutirostris* was consumed only during the wet season, while the consumption of *Pimelodella* sp. was much higher during the dry season, and that of *G. brasiliensis* was slightly higher during the dry season. In any case, consumption of

H. malabaricus and the exotic *C. rendalli* was frequent and abundant throughout the year, demonstrating a marked preference for these two species.

We observed that the otters in the SLBS showed a feeding preference for low-mobility, sedentary, and abundant fish with higher biomass. Regarding behavior, we can list the following in order of importance: low mobility and high frequency/abundance, high mobility and high frequency, low mobility and low frequency.

We also found that biomass has a preponderance on prey selection over abundance. Therefore, more nutritious and abundant prey that require less energy expenditure to be captured will be consumed. This is because the cost-effectiveness of foraging and ease of capture are important factors for improving predator survival (Pianka 2011). Thus, otters tend to forage optimally, seeking to minimize energy expenditure while capturing their prey (Rheingantz et al. 2012).

This food preference can be explained through the optimal foraging theory (OFT), an evolutionary trait that correlates the success of survival and reproduction of a species to the optimal use of resources available, like food. In this case, the nutritional characteristics of the prey, including biomass and caloric input, as well as ethological characteristics, such as the ability to escape, are considered when analyzing whether the predator has optimized foraging (Thompson and Stelle 2014). In this sense, otters can be considered efficient foragers according to the OFT criteria.

Thompson and Stelle (2014) tested the OFT in captive animals in their study with *Lontra canadensis* (Schreber, 1777) from the Seneca Park Zoo, Rochester, USA. The authors found that otters exhibited a preference for the consuming species that provided significantly more calories per unit of time. Therefore, these animals preferred large prey, even if the energy cost for their capture was higher, which Thompson and Stelle (2014) attributed to the gain of greater caloric intake per unit of prey. Another advantage would be thermoregulation, given the energy savings the animal would retain when staying out of the water for longer periods while consuming their prey. These same authors found that fish that were more difficult to capture but easier to handle and consume were preferred over species of similar size that were easier to capture but had a body circumference and spines on the fins that would make handling and consumption difficult. With this, Thompson and Stelle (2014) concluded that North American river otters preferred species with specific morphology, even of equal size, to other species that are easier to capture but more difficult to handle, which corresponds to the OFT predictions since prey selection maximized the net energy obtained after accounting for the metabolic costs of foraging.

Crustaceans are widely reported in the literature as a representative food item in the diet of many populations of otters (Pardini 1998, Quadros and Monteiro-Filho 2001, Quintela et al. 2008, Carvalho et al. 2010b, Rheingantz et al. 2012). The high consumption of *T. fluviatilis* may be related to its abundance and relatively low capacity for escape (Pardini 1998), especially during its reproductive cycle, which occurs at the beginning of the rainy season (Costa-Neto 2007). During this period, *T. fluviatilis* may be more vulnerable, thereby facilitating its capture by otters. This corroborates our data since crustaceans were mainly found in fecal samples collected during the rainy season.

We observed that amphibians, reptiles (ophidians), and birds were seldom consumed by otters, which is in accordance with previous studies on their diet (Andrade and Helder-José 1997, Pardini 1998, Quadros and Monteiro-Filho 2001, Kasper et al. 2004). Although uncommon and not recorded in the present study, mammal parts have also been found in otter fecal samples. Quintela et al. (2008) recorded the presence of the capybara *Hydrochoerus hydrochaeris* (Linnaeus, 1766), and Quintela and Gatti (2009) the presence of armadillo (Cingulata: Dasypodidae) in otter feces, therefore demonstrating the occasional consumption of other taxa.

The sampling area in SLBS was limited due to access to samples; therefore, we may have sampled a small number of individuals, considering the linear density of the species of approximately one individual per kilometer (Trinca et al. 2013). This limitation may bias the extrapolation of eating habits to the entire SLBS population, as the occurrence of high intraspecific food specialization of otters in the same population must be considered, with food variation associated with temporal, spatial variables, and individual diet specializations (Carrasco et al. 2020).

Environment quality and otter diet

The degradation of aquatic habitats is one of the consequences of anthropogenic modification of the environment (Reis 2013). In addition to the pollution and unhealthy conditions of the water in the Timbuí River, part of the garbage from the urban area is retained by the vegetation on the riverbanks along the entirety of the SLBS (Mendes and Padovan 2000, Louzada and Fonseca 2002, Bernabé (2003) and our field observations). Sarmento-Soares and Martins-Pinheiro (2010) reported the persistence of the anthropogenic influence in the Timbuí River even after implementation of the sewage treatment plant; as a matter of fact, finding garbage and oil stains in the river is still commonplace. Sarmento-Soares and Martins-Pinheiro (2010) suggest that the persistent pollution along the Timbuí River may have compromised the integrity of its ichthyofauna. Official data from the Companhia Espírito Santense de Saneamento (Sewage Company of the Espírito Santo; CESAN) suggest a low level of adherence of many of the residents to the sewerage system in Santa Teresa; as a result, urban effluents are still being released into the Timbuí River, a situation that is aggravated during the dry season (CESAN 2017).

Habitat destruction and species introduction are among the main threats to vertebrate extinction, where specialists or poorly tolerant species are the most vulnerable to environmental adversities (Diamond 1984, Marshall 1988). Even if ecosystem services are maintained, biodiversity reduction can threaten the maintenance of viable populations of many different species since low genetic diversity represents a major limitation for them to respond to various threats and changes in the environment (Naeem et al. 2012). Consequently, there may be a decline in the functioning ecosystems and their stability (Naeem et al. 2009, Isbell 2010).

The reduction in the volume of prey and/or water pollution can interfere with otter distribution, even if the level of disturbance the species tolerates is difficult to assess (Quadros 2009). Neotropical otters might have a certain tolerance to anthropogenic environments since they can be found in degraded environments (Rheingantz et al. 2011, Rodrigues et al. 2013), provided sufficient resources are available to support its populations (Carvalho-Junior 2007). However, Rheingantz et al. (2014) found that protected areas are more suitable places for the long-term population viability of otters, especially in large areas where human disturbances are minimized.

Regarding the diversity of the ichthyofauna in the SLBS, Bernabé (2003) found that the indices of diversity and species richness were relatively low throughout the year in the area, suggesting that the ichthyofauna of the Timbuí River may be constituted by only a few species practically all months. Therefore, the low diversity of fish in the composition of otters' diet in the SLBS, with a predominance of generalist species and with high environmental plasticity, may indicate the influence of water quality on local ichthyofaunal diversity.

Although the SLBS provides sufficient subsidies for the presence and maintenance of otter populations, this is only because the area still offers shelter, low human disturbance, and areas suitable for refuge and reproduction, in addition to sufficient food stocks necessary for their survival, even though such stock comprises generalist species that are tolerant to environmental changes.

This way, the otters from the SLBS demonstrated a preference for slow and sedentary fish. Prey selection considered the cost-benefit between the energy expenditure required to obtain the prey in relation to the energy supply provided by it; accordingly, factors of abundance, biomass, and prey behavior were counterbalanced. This may explain the record of highly agile prey in the otters' diet, provided their high abundance. In order of importance, the most preyed fish present: i. low mobility and high abundance in the environment; ii. high mobility and high abundance; iii. low mobility and low abundance. Such behavior demonstrates the otters' high predatory efficiency, optimizing their energy expenditure while foraging. This is in line with OFT premises, in which prey selection maximizes the net energy obtained when counterbalanced with the metabolic costs of foraging.

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