



# Feeding behavior and trophic niche partitioning between co-existing river otter species

Carine G. Moraes · Jensen Hegg · Tommaso Giarrizzo · Marcelo C. Andrade

Received: 2 July 2020 / Revised: 28 April 2021 / Accepted: 3 May 2021  
© The Author(s), under exclusive licence to Springer Nature Switzerland AG 2021

**Abstract** Niche partitioning occurs among coexisting populations to reduce the effects of competitive exclusion among species of similar niche. The aim of the present study is to verify the trophic niche partitioning and feeding behavior between two mustelids, the Giant otter and the Neotropical otter, through the dry and rainy season hydrologic of the Lower Xingu River. Our results suggest that the diets of both mustelids are composed primarily of fish of the family Anostomidae (Headstanders). Despite extensive niche overlap, our results indicate partitioning is facilitated by differences in niche breadth, with potential implications for conservation of both species in the case of declines in prey abundance and diversity. Both species inhabit an area recently impacted by

completion of the Belo Monte Hydropower Plant, resulting in large changes to the hydrologic regime. Thus, our results provide important information for conservation efforts regarding the feeding behavior and co-occurrence of both species, as well as providing a baseline for monitoring future health of these mustelid populations. The present study is the first to test the hypothesis of niche partitioning between these two mustelids outside a protected area in the Amazon.

**Keywords** Neotropical otter · *Lontra longicaudis* · Giant otter · *Pteronura brasiliensis* · Diet · Xingu River

---

Handling editor: Stuart Halse

---

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10750-021-04614-w>.

---

C. G. Moraes (✉) · T. Giarrizzo · M. C. Andrade  
Núcleo de Ecologia Aquática e Pesca da Amazônia,  
Laboratório de Biologia Pesqueira e Manejo de Recursos  
Aquáticos, Universidade Federal do Pará, Avenida  
Perimetral, 2651, Terra Firme, Belém,  
PA 66077-830, Brazil  
e-mail: carinemoraes8@gmail.com

J. Hegg  
Department of Fish and Wildlife Sciences, University of  
Idaho, Moscow, ID 83844-1136, USA

## Introduction

Many aquatic and semi-aquatic animals use the resources of several habitats within freshwater ecosystems during their life cycles (Schofield et al., 2018). This is particularly true in the Amazon region, where species shift resources, habitat, and behavior in response to seasonal cycles of flooding which often drastically alter their riverine environment (Cabral et al., 2010; Rheingantz et al., 2011). In these cases, species often change their activity patterns in response to environmental factors such as weather and spatiotemporal distribution of resources (Daura-Jorge et al., 2005; Groenendijk et al., 2014; Fitzgerald et al.,

2018). Low water periods, however, often concentrate species into smaller geographic areas, forcing species with similar niches to share resources (Andrade et al., 2019).

Theory predicts, and studies have shown, that in cases of this type of co-occurrence, niche partitioning occurs between the coexisting populations, reducing competition and allowing the coexistence between species with similar ecological requirements (Bonesi et al., 2004; Papastamatiou et al., 2006; Gallagher et al., 2017). In addition, resource partitioning reduces the probability of competitive exclusion occurring among species (May, 1974; Pianka, 1974; Wiens et al., 2010). A species can adapt its behavior in response to competition, widening or narrowing its diet to reduce any niche overlap among coexistent species (Gotelli & McCabe, 2002; Araújo et al., 2011). This balance of competition and resource partitioning helps to maintain community structure and the niche of the organisms involved (Krebs, 1999).

One example of seasonal shifts leading to sympatric habitat occupation of species with similar niches occurs in Amazonian mustelids, whose habitats and species exploitation patterns shift with seasonal resource availability (Pardini, 1998; Rheingantz et al., 2011; Leuchtenberger et al., 2015; Hernández-Romero et al., 2018). The Neotropical otter *Lontra longicaudis* (Olfers, 1818) (hereafter *Lontra*), and the Giant otter *Pteronura brasiliensis* (Zimmermann, 1780) (hereafter *Pteronura*), co-occur in the changing riverine environment of the Amazon basin and share great similarities in their feeding behavior and preferred habitat (Carter & Rosas, 1997; dos Reis et al., 2011; Muanis & Oliveira, 2011; Silva et al., 2013).

Both are semi-aquatic, carnivorous mammals of the family Mustelidae and subfamily Lutrinae, with fish as their main food source (Silva et al., 2013; Groenendijk et al., 2014). *Lontra* is characterized by its brown coloration and body size ranging from 1.2 to 1.4 m. They are elusive, diurnal, and generally solitary, forming mating or family groups composed of female and male, or female and juveniles, only during the breeding season (Rheingantz et al., 2014, 2017). *Pteronura* is the largest otter of the family, reaching a total body length up to 1.8 m, its body is predominantly dark brown and can be further distinguished by a yellowish-brown patch on the throat. *Pteronura* is diurnal as well, but is a more social species than

*Lontra*, living in groups that include females, males and pups (Carter & Rosas, 1997; Duplaix et al., 2015). Both species are also top predators in the food chain, acting as a top-down control on prey populations, and for this reason their presence is a good indicator of ecosystem health (Duplaix et al., 2015; Trigila et al., 2015).

Studies of habitat occupation and use by tropical mustelids during the different seasons of the year are still scarce, but it is believed that during the rainy season both species leave their dry season territories, or extend those territories toward wetlands, looking for fish (Carter & Rosas, 1997; Leuchtenberger et al., 2013, 2015). Thus, seasonal differences in feeding behavior between mustelids throughout the year are related largely to differences in prey availability (Leuchtenberger et al., 2013; Krpo-Cetkovic et al., 2019). The rainy season, although a period of increasing resource availability for many aquatic Amazonian species, is a difficult period for otters to find prey due to prey dispersion into the environment (Leuchtenberger et al., 2015; Fitzgerald et al., 2018). It is unknown to what degree the feeding behavior and trophic position overlap between these species during this low-resource period. Predators, such as otters, are typically generalists, feeding on a variety of prey and often exploiting the most energy rich resources (“optimal foraging theory” e.g. Emlen, 1966; MacArthur & Pianka, 1966; Charnov, 1976), with interspecific competition intensifying between species when resources are reduced (Andrade et al., 2019). In this sense, the diet evaluation of an organism is important for understanding of the trophic interactions among coexistent species (Sih & Christensen, 2001; da Silva et al., 2017). This is particularly true for top predators, which can affect the top-down population dynamics of the ecosystems in which they reside. Thus, understanding the niche dynamics of *Lontra* and *Pteronura* is important in a theoretical context, as an example of niche partitioning in large predators, as well as from an ecosystem perspective within the Amazon region.

Characterizing the ecological dynamics of these species is also important because these mustelid species are heavily affected by anthropogenic actions. Both species are experiencing population declines through habitat loss, such as river depredation and removal of riparian forests, changes which are also causing reductions in fish populations and thus

reductions in prey availability (Rheingantz et al., 2014; Duplais et al., 2015; Rheingantz & Trinca, 2015). These effects threaten the conservation status of both species. *Pteronura* is classified as a “vulnerable” species in Brazil (Instrução Normativa Interministerial, 2012) and “endangered” by the International Union for Conservation of Nature (IUCN) (Groenendijk et al., 2015). Similarly, *Lontra*, while not listed on the Brazilian list of threatened species (Instrução Normativa Interministerial, 2012), is classified as “near threatened” by the IUCN (Rheingantz & Trinca, 2015).

Understanding niche dynamics between these species is crucial for conservation of one or both species where they co-occur. This is particularly true given the environmental effects of the Belo Monte Hydropower Plant (HPP), construction of which concluded in the Lower Xingu River in 2016, and which is likely to directly impacts the habitat of both species and reduce their main food source (Silva et al., 2013; Groenendijk et al., 2014; Fitzgerald et al., 2018; Andrade et al., 2019). This study was conducted prior to the completion of the dam, providing the only available baseline understanding of the trophic dynamics of both species outside conservation areas in Brazil.

We hypothesized that these mustelids coexist through trophic niche partitioning, despite clear overlap in feeding behavior, seasonal habitat use, and resource use. Specifically, we hypothesized that differences in their diets allow them to co-occur in the same area using similar prey. This study aims to: (i) characterize the feeding behavior of *Lontra* and *Pteronura* in the lower Xingu River; (ii) estimate the niche breadth and trophic specialization of each mustelid through diet analysis; (iii) identify the importance of alimentary items in diet for each mustelid species; and (iv) analyze the seasonal variations in the feeding behavior and prey selection of mustelid species between the rainy and dry seasons.

## Methods

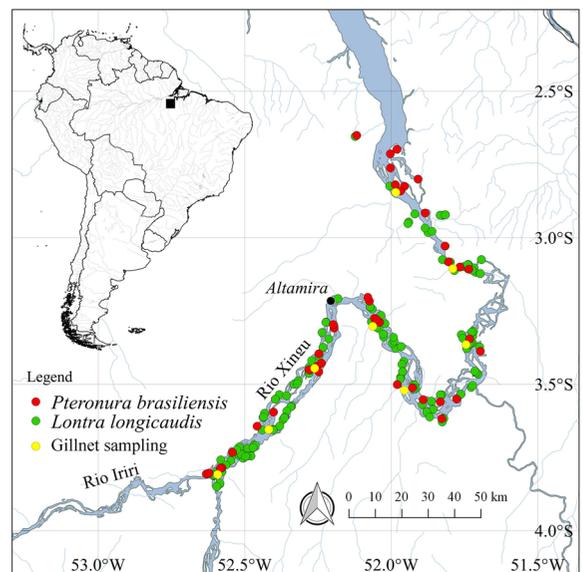
### Study area

The present study was carried out in the Xingu River, one of the largest tributaries on the right (southern) bank of Amazon River, extending approximately

2,050 km (Andrade et al., 2019). The Xingu is a “clearwater” river (sensu Junk et al., 2011), with low concentrations of suspended material and nutrients, poor in phytoplankton, and dependent on allochthonous sources such as alluvial forest on its islands and river margins for much of its productivity (Camargo & Ghilardi, 2009). The weather is characterized as tropical, warm, and humid with annual temperatures ranging from 25 to 27°C. Its waters show volumetric flow variations between 8,000 and 10,000 m<sup>3</sup>/s in the rainy season (between December and May), and 2,000 m<sup>3</sup>/s in the dry season (between June and November) (Camargo & Ghilardi, 2009).

### Sampling

The sampling area was roughly 300 km long, beginning upstream at the confluence of Iriri and Xingu Rivers and continuing downstream to the city Senador José Porfírio (Fig. 1), encompassing the entirety of the Belo Monte HPP. Collection of fecal samples from *Lontra* and *Pteronura* was performed in two hydrologic seasons. August 2012 represented the dry season and February 2013 the rainy season. The sampling areas were traveled with the use of small motorized vessels, surveying the margins looking for traces of



**Fig. 1** Sites of fecal sampling of *Lontra longicaudis* and *Pteronura brasiliensis* and gillnets sampling collected in dry (August 2012) and rainy (February 2013) seasons throughout the Xingu River basin

feces. Samples of *Lontra* generally are found on the rocks, tree trunks, and sand banks, or near to its burrow entrance. *Lontra* feces are cylindrical shaped and more consistent than the *Pteronura* feces (Kasper et al., 2008; Silva et al., 2013). *Pteronura* feces are generally found in community latrines, scattered on the ground of river banks where the species remove the vegetation along the margins of rivers (Carter & Rosas, 1997). The samples from the same latrine of the same *Pteronura* group in the same season were combined, because according to Leuchtenberger & Mourão (2009) *Pteronura* defecate in community latrines, scattering the soil and mixing its feces, which makes it impossible to identify the feces from different individuals. This procedure guarantees the independence of samples (Leuchtenberger et al., 2020). In the field, each collected sample was packaged in individual plastic jars, given an alphanumerical code identifying the place of collection, date and species (*Lontra* or *Pteronura*).

#### Diet analysis

For diet analysis, fecal samples were washed individually in running water using a 1 mm mesh sieve which retained undigested food items in the feces which allow identification (e.g., scales, otoliths, bones, exoskeletons, teeth, fur, and others). These samples were then dehydrated in an oven at 60°C and examined under a ZEISS model Stemi DV4 stereoscope. The items were grouped and identified using specific literature and/or comparing with biological samples in the fish collection of the Grupo de Ecologia Aquática (GEA) at the Universidade Federal do Pará (UFPA).

#### Data analysis

The importance of food resources  $A_i$  was evaluated using the alimentary index of Kawakami & Vazzoler (1980):

$$A_i = Fi * Ni / \sum(Fi * Ni),$$

where  $Fi$  is the frequency of occurrence of the prey  $i$  and  $Ni$  is the numerical frequency of the prey  $i$ . The frequency of occurrence ( $Fi$ ) is the relative frequency of occurrence of the prey  $i$  in relation to the number of analyzed samples, and the numerical frequency ( $Ni$ ) represents the relative number of the prey  $i$  in relation

to the total number of prey. In order to be conservative, multiple items such as scales of a particular fish or crab exoskeleton in the same scat were pooled and counted as just one individual of that group. The similarity in diet composition between mustelids was evaluated through a cluster analysis using Bray–Curtis distance based on the matrix of the alimentary importance of the items found, and graphically represented with a heatmap (Clarke et al., 2014).

The niche breadth and niche overlap between species and between seasons were inferred based in the Levin's niche breadth ( $B$ ) (Krebs, 1999):

$$B = 1 / \left( \sum P_j^2 \right), \text{ followed by } B_i = (B - 1) / (n - 1)$$

where  $P$  is the proportion of scats where the resource  $j$  was found,  $B_i$  is the standardized niche breadth, and  $n$  is the number of possible food resources. The niche overlap of species was calculated using Pianka's index with the null model based in the algorithm RA3 available in the R package EcoSimR v1.0 (Gotelli & Ellison, 2013) and 9,999 Monte Carlo permutations.

To reveal feeding patterns of selection in *Lontra* and *Pteronura*, a Principal Coordinate Analysis (PCo) was made with the Bray–Curtis dissimilarity matrix of diet data of the two mustelids between rainy and dry seasons, and potential differences tested as Permutational Multivariate Analysis of Variance (PERMANOVA) with 9,999 permutations in PRIMER v.7 (Clarke & Gorley, 2015).

#### Resource availability

The alimentary resource availability, more specifically fish availability, since they are the majority of consumed prey resources in both mustelids (Silva et al., 2013), was estimated based on gillnet samples collected at the same sites and during the same periods as which fecal samples were collected (data provided by Norte Energia S.A.). Three sets of seven gill nets were used, each set having net sizes between 2 and 18 cm of mesh. The nets were 20 m long and 2 m deep. Gillnets were set at random locations at twilight near the river margins (Fig. 1) and remained there for a 14 h period. Nets were checked every 3 h to avoid losses by predation.

The potential selection of prey by the two mustelids was evaluated by the Ivlev's Electivity Index ( $E_i$ ), calculated as:

$$E_i = (r_i - n_i) \div (r_i + n_i),$$

where  $r_i$  is the proportion of a particular fish family in the diet of mustelids, and  $n_i$  is the proportion of a particular fish family collected by gillnets. The  $E_i$ 's values range from  $-1$  to  $+1$ , where the negative values indicate a less accessible prey or rejection of them, zero indicates random feeding, and positive values indicate active search for prey (Strauss, 1979).

### Trophic connections between mustelid species

To evaluate the trophic connections between *Lontra* and *Pteronura*, and between the rainy and dry seasons, bipartite networks were created from the data. The bipartite networks represent the trophic linkages between the mustelids (consumers) and the food items (resources) using the package 'bipartite' (Dormann et al., 2008) in R (R Development Core Team, 2019).

To analyze the influence of seasons the trophic connections of the two mustelids were also calculated by two methods. Connectance (C) was calculated as the proportion of interactions in relation to all possible interactions (Dunne et al., 2002; Thompson et al., 2012). In this context, species with C near zero (0) are considered trophic specialists, while those near to one (1) are trophic generalists. Secondly, linkage density (D) was calculated for each species. Linkage density is the average number of linkages by species (Vermaat et al., 2009; Thompson et al., 2012), calculated by:

$$D = L/S,$$

where  $L$  is the number of links, and  $S$  is the number of knots according to Dormann et al. (2008).

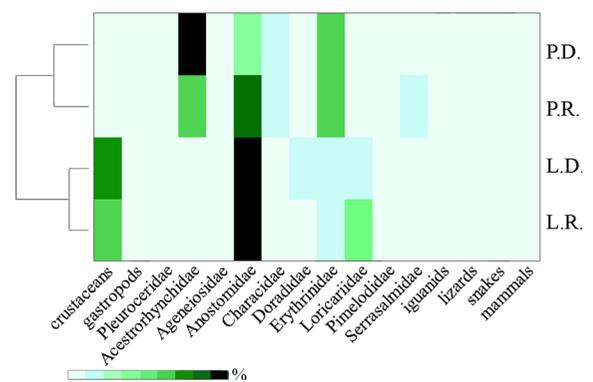
## Results

Overall, 216 fecal samples of mustelids were collected throughout the Lower Xingu River basin. Of these, for *Lontra* 56 were samples from the rainy and 114 from dry season. For *Pteronura*, 30 samples were collected from the rainy and 16 from the dry season. For all samples we classified prey to five large food groups: crustacean, gastropod, fish, reptile and mammal. These five groups were made up of 16 item categories, the majority being fish families. The groups present in the sample were crustaceans, gastropods, Pleuroceridae, fish (Acestrorhynchidae, Ageneiosidae,

Anostomidae, Characidae, Doradidae, Erythrinidae, Loricariidae, Pimelodidae, Serrasalminidae), iguanids, lizards, snakes, and mammals. We kept the groups iguanids, lizards and snakes separated rather than together in the higher taxa level Squamata, as well as Pleuroceridae rather than together in the gastropods to evidence specificity in diet of each mustelid.

Based in the alimentary index, *Lontra* fed most on fish in the family Anostomidae and on Crustacea in both seasons. *Pteronura* fed most on the fish families Acestrorhynchidae and Erythrinidae in the dry season and on Anostomidae and Acestrorhynchidae in the wet season (Online Resource 1). The similarity in diet between mustelid species was indicated by a dendrogram generated from the cluster analysis of the importance of each prey item (Fig. 2). The result revealed two distinct groups by similarity of alimentary importance: Group 1 (*Pteronura* in the dry and rainy seasons) and Group 2 (*Lontra*—in the dry and rainy seasons). Further, the analysis confirmed the result above that *Pteronura* fed most on the fish family Acestrorhynchidae in the dry season and on the fish family Anostomidae in the rainy season. In contrast, *Lontra* mainly consumed fish in the family Anostomidae in both periods.

The niche breadth analysis indicated that both mustelid species show wider niche breadth in the rainy season than in the dry, and *Lontra* showed wider niche than *Pteronura* in both seasons (*Lontra*:  $B_{dry} = 0.36$ ,  $B_{rainy} = 0.42$ ; *Pteronura*:  $B_{dry} = 0.11$ ,  $B_{rainy} = 0.28$ ). The diet comparison using Pianka's index based on the



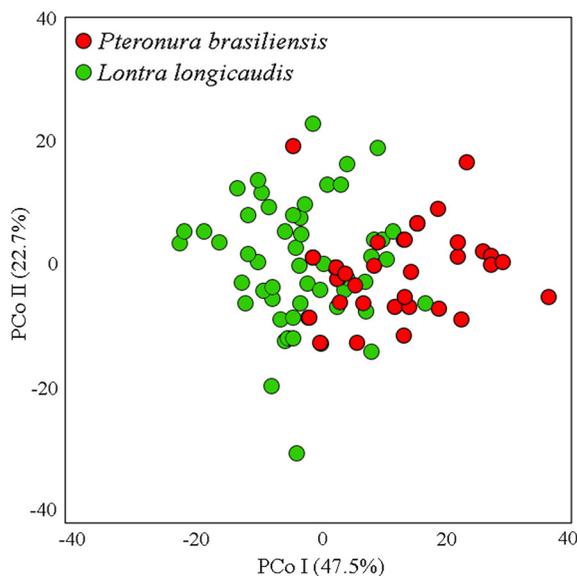
**Fig. 2** Cluster analysis and heatmap showing the similarity in diet of the two mustelid species *Pteronura brasiliensis* and *Lontra longicaudis* between seasons of dry (Aug/2012) and rainy (Feb/2013) from Xingu River basin. P.D (*P. brasiliensis*—Dry); P.R (*P. brasiliensis*—Rainy); L.D (*L. longicaudis*—Dry); L.R (*L. longicaudis*—Rainy)

niche breadth of species showed low interspecific niche overlap in dry season ( $O_{jk} = 0.28$ ) whereas niche overlap was high in the rainy season ( $O_{jk} = 0.55$ ). In addition, the observed niche overlap was greater than that estimated by the null model (observed = 0.59 > estimated = 0.32). The diet comparisons between dry and rainy seasons did not find significant statistical differences for *Lontra* (PERMANOVA, *Pseudo-F*: 0.53,  $p = 0.69$ ) or for *Pteronura* (PERMANOVA, *Pseudo-F*: 0.86,  $p = 0.48$ ). The PCo explained 70.2% of the alimentary pattern in the first two axis (Fig. 3), 47.5% in the first axis and 22.7% in the second, unveiling two distinct groups, one corresponding to *Lontra*, whether in dry or rainy season, and other composed by *Pteronura*, whether in dry or rainy season (PERMANOVA, *Pseudo-F*: 16.81,  $p < 0.0001$ ). The results showed significance for the alimentary items only for two large groups, fish and crustaceans. For both mustelids the majority of the significance was due to fish families Acestrorhynchidae, Anostomidae, Characidae, Erythrinidae, Loricariidae and Serrasalminidae, and also to the group Crustacea, which is composed mostly of freshwater crabs (Online Resource 2).

Overall 4,498 fish specimens belonging to 10 taxonomic orders, 33 families and 168 species were

collected during the sampling with gillnets in both seasons (Online Resource 3). From those, 2,028 fish of 30 families were collected in the dry season, and 2,470 fish of 27 families in the rainy season. The relative abundance of eight fish families (Online Resource 4) which were also found in the mustelids diet was evaluated. The Ivlev's electivity index (Ei) showed greater preference for particular fish families (Online Resource 5) for both mustelids. *Lontra* in the dry season actively feed on (positively selected) five fish families; while randomly feed (neutral selection) on three families. Conversely, in the rainy season *Lontra* actively sought seven fish families, which in the dry season were randomly consumed (Fig. 4). *Pteronura* actively feed on four fish families in the dry season as shown by the electivity index, while also randomly consuming four families in this season. On the other hand, *Pteronura* showed active consumption for seven fish families in the rainy season; and only the family Loricariidae was randomly consumed during this season (Fig. 4).

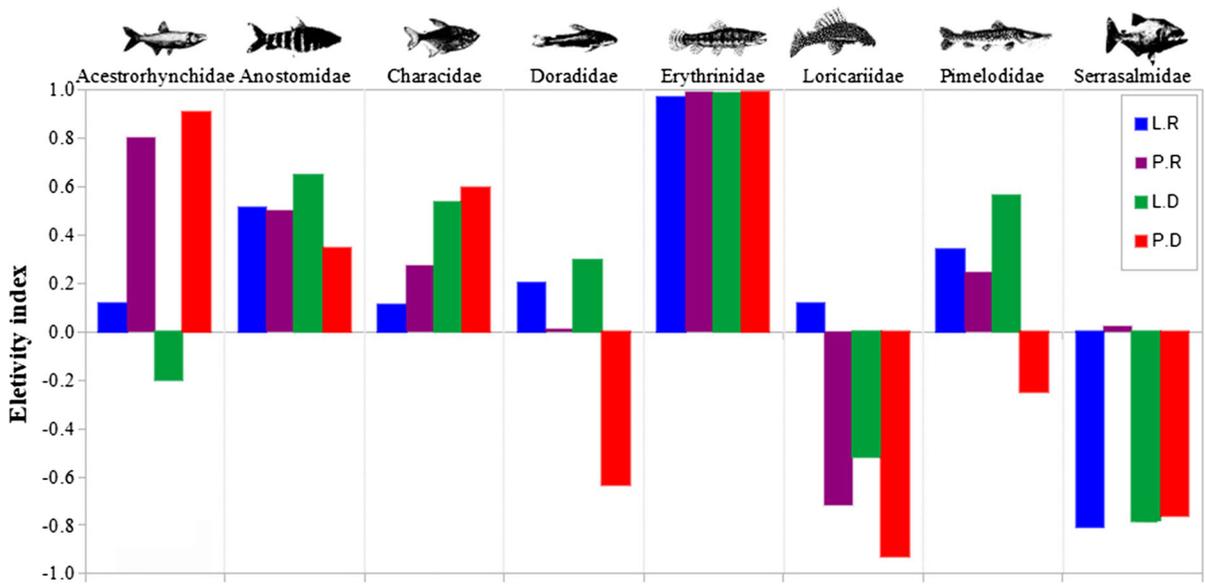
The results suggested high trophic connection between mustelids ( $C_{dry} = 0.86$ ;  $C_{rainy} = 0.79$ ), suggesting opportunistic and generalist behavior in resource choice for both species. In Fig. 5 the bipartite net represents the predator–prey interactions of the mustelids and their food resources. The horizontal bars in the top represent the niche breadth of each mustelid in its respective season. The horizontal bars in the bottom represent the resource availability for mustelids of the respective prey. The linkages are different, thickness represents the importance of each prey for the mustelid in determined season being the wider linkage more important and narrower less important.



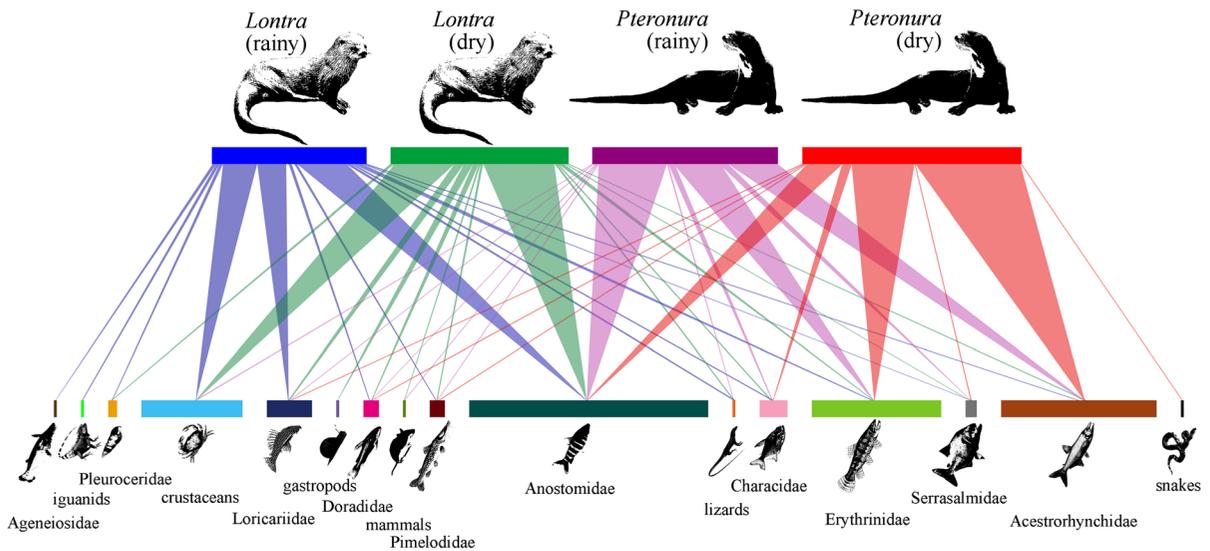
**Fig. 3** First two axes of the principal coordinates analysis (PCo) based on diet contents of the two mustelids (P) *Pteronura brasiliensis* and (L) *Lontra longicaudis*, during dry (Aug/2012) and rainy (Feb/2013) seasons in the Xingu River basin

## Discussion

Several prior studies have suggested that seasonal changes shape the feeding behavior of mustelid species, mainly due to changes in prey availability (e.g., Pardini, 1998; Rheingantz et al., 2011; Leuchtenberger et al., 2015; Krpo-Cetkovic et al., 2019). However, our study did not find major differences in mustelids' diet within each species between seasons. Diet comparisons between the two mustelid species showed lower niche overlap during the dry season. This may be explained by the high availability of a variety of resources in the environment during this



**Fig. 4** Prey electivity of fishes by the two mustelids (*Lontra longicaudis* and *Pteronura brasiliensis*) from Xingu River basin during seasons of dry (Aug/2012) and rainy (Feb/2013)



**Fig. 5** Bipartite network diagram representing the predator–prey interactions between *Lontra* and *Pteronura*. Predators are represented above by the two mustelids *Pteronura* and *Lontra* from seasons of dry (Aug/2012) and rainy (Feb/2013); and prey

are represented below. The bar width of predators represents the niche breadth and the bar width of prey is the level of importance to the diet of both mustelids

low-water season, allowing each mustelid to access the prey of its preference (Silva et al., 2013).

The highest niche overlap occurred in the rainy season, likely owing to the greater dispersion of food resources (e.g., fishes) into flooded riparian areas, resulting in lower capturability by the mustelids and,

thereby, forcing both predators to feed on the most accessible, abundant, and similar prey. However, despite the niche overlap, the trophic partitioning between the two mustelids was facilitated by the wider niche breadth of *Lontra*. Wider niche breadth presumably prevents competitive exclusion between species,

providing niche differentiation among species and optimizing their coexistence (Schirmer et al., 2020). This supports the hypothesis of resource partitioning between *Pteronura* and *Lontra* through niche distinction. The same mechanism has been recorded for other mustelid species, for example the Eurasian otter *Lutra lutra* and the American mink *Mustela vison* (Bonesi et al., 2004). In this example, *M. vison* broadened its diet and consumed greater proportions of birds and mammals in the presence of *L. lutra*.

The feeding behavior and prey choice of both *Pteronura* and *Lontra* in the present study is consistent with optimal foraging theory (MacArthur & Pianka, 1966). Generally, these animals are opportunistic predators, actively seeking the most vulnerable or most abundant prey in the environment, this includes fishes of the family Anostomidae (headstanders), the main food resource for both mustelids in this study. These fish form large schools with multiple species of similar morphology (Sidlauskas & Birindelli, 2018), as well as the fishes of the family Acestrorhynchidae (smallscale pike characins; the second most consumed food resource of *Pteronura*). Both fish families are pelagic fishes and represent a large portion of the biomass found in Amazonian aquatic environments (Garavello & Britski, 2003; Menezes, 2003).

While benthic fishes, with low mobility and consequently greater vulnerability to predators (Armbruster et al., 2018), make up a significant part of each species diet, the two mustelids do not prey equally on all present benthic species. Fishes of the family Loricariidae (plecos) are consumed in abundance by *Lontra*, while the fishes of the family Erythrinidae (trahiras), which are composed of sedentary species (Oyakawa & Mattox, 2018) were more commonly consumed by *Pteronura*.

Since the mustelids utilize the terrestrial environment, performing feeding, reproduction, shelter building, and other activities on river banks (Alarcon & Simões-Lopes, 2003), crustaceans (freshwater crabs) have been shown to be an important group in the diet of *Lontra* in some studies (Rheingantz et al., 2011; Quintela et al., 2012), but less important in others (Silva et al., 2013; Souza et al., 2013). Our study indicated that crustaceans made up a significant part of the diet of *Lontra*, and this was a key differentiator between the diets of the two species. Crustaceans were rarely found in the diet of *Pteronura*.

The comparison of diet with prey availability from gillnet captures found that among the eight fish families analyzed, *Lontra* showed feeding preference for five of those fish families during the dry season, and seven during the rainy season. Silva et al. (2013) suggest that both mustelids have a preference for prey with low mobility. That is, fish with reduced escape ability, such as the fishes of the family Erythrinidae. In our study this family showed positive selectivity and was consumed in abundance by both mustelids. However, this family was also poorly represented in gillnet captures, potentially biasing these results. Low captures are likely due to the methodology used, since gillnets are most suitable for catching more active, pelagic fishes (Mesquita et al., 2019). The consumption of other food items such as Pleuroceridae, iguanids, lizards and mammals (small rodents) has been reported in previous studies on diet of mustelids (Silva et al., 2013; Souza et al., 2013; Krpo-Cetkovic et al., 2019). Even though these prey appeared in the present study, they were less important in diet for both mustelids, appearing mainly in the rainy season. This is explained by weather conditions in the rainy season when weather conditions made their main prey items more difficult to catch (i.e., fishes) for both mustelids (Pardini, 1998) and supports the finding that both species are forced to broaden their niche during the rainy season.

Beyond facilitating their co-occurrence ecologically, understanding the niche differences between the *Lontra* and *Pteronura* may provide important insights useful for mitigating the poor current conservation status of both species. Understanding the biological and ecological needs of each species helps ensure the most effective measures for conservation of these animals in their natural environment. We saw that, while both mustelids exhibit generalist feeding behavior, *Pteronura* have a narrower niche when compared to *Lontra*. This suggests that *Pteronura* may be more sensitive than *Lontra* to environmental changes such as fragmentation and habitat loss, which cause decreases in resource availability. In fact, the effect of anthropogenic changes on its narrower niche breadth, in addition to its diurnal behavior and resultant heavy hunting pressure for its fur, may be a reason for the status of *Pteronura* as a “Threatened” species while *Lontra* is only listed as “Near Threatened” by the IUCN.

Our results indicate that *Pteronura* would suffer more severely in conditions of low-resource availability, especially decreases in fish diversity and abundance. Despite often displaying generalist feeding behavior, the diet of *Pteronura* is nonetheless more specialized to fish consumption than *Lontra*. This scenario of decreased fish diversity and habitat fragmentation (which is known to decrease species diversity) was predicted as a result of the construction of the Belo Monte HPP (Sabaj Pérez, 2015). This indicates that *Pteronura* may be more heavily affected by the environmental changes the Belo Monte dam complex has brought to the Xingu River. However, despite these threats, strategies for the conservation of mustelids in the region are lacking (Groenendijk et al., 2015; Rheingantz & Trinca, 2015).

The present study is the first to test the hypothesis of niche partitioning between these two mustelids outside a protected area in the Amazon. The two mustelid species reduce niche overlap during the dry season by some dietary specialization. However, niche overlap occurs during the rainy season when food is comparatively scarce. In this context, and despite the limitations related to the small sample size, our study provides critical baseline information on the feeding behavior and niche partitioning of both mustelid species prior to the completion of the Belo Monte HPP. Evidence from our analysis indicates that *Pteronura* may be more impacted by the predicted fish diversity loss after construction of HPP, an issue that should be investigated by future studies. Both species are top predators of major importance for nature conservation and are keystone species within their aquatic communities. Understanding their ecology, both before and after anthropogenic impacts on their populations, is critical to their conservation.

**Acknowledgements** CGM was funded by Coordination for the Improvement of Higher Education Personnel (CAPES); JH was funded by a Fulbright Post-Doctoral grant, Fulbright Commission Brazil; TG receives productivity grant from the National Council for Scientific and Technological Development (CNPq # 311078/2019-2), and MCA is funded by National Program for Post-Doctoral (PNPD/CAPES # 2017-6; financial code 001). This article was developed at the Aquatic Ecology and Fisheries Post-Graduate Program of the Federal University of Pará (PPGEAP/UFPA) as the Master Dissertation of the first author. This study was funded by Norte Energia S.A. and Fundação de Amparo e Desenvolvimento da Pesquisa (FADESP).

**Author contributions** Carine G. Moraes, Tommaso Giarrizzo and Marcelo C. Andrade contributed to the study conception and design. Material preparation, data collection and analysis were performed by Carine G. Moraes, Tommaso Giarrizzo, and Marcelo C. Andrade. The first draft of the manuscript was written by Carine G. Moraes and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

**Funding** Coordenação de Aperfeiçoamento de Pessoal de Nível Superior Finance Code 001, and by PROPESP/UFPA; Fulbright Commission Brazil; Conselho Nacional de Desenvolvimento Científico e Tecnológico.

**Availability of data and material** We declare that all data in this scientific manuscript will be available upon request.

**Declarations**

**Conflict of interest** There is no conflict of interest to declare.

**Ethical approval** Not applicable, all data including animal subjects were conceded by Norte Energia S.A., the company authorized by the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA) to collect at the Xingu River in the area of influence of the Belo Monte Hydropower Plant.

## References

- Alarcon, G. G. & P. C. Simões-Lopes, 2003. Preserved versus degraded coastal environments: a case study of the Neotropical otter in the Environmental Protection Area of Anhatomirim, Southern Brazil. *Group Bull* 20: 6–18.
- Andrade, M. C., D. B. Fitzgerald, K. O. Winemiller, P. S. Barbosa & T. Giarrizzo, 2019. Trophic niche segregation among herbivorous serrasalmids from rapids of the lower Xingu River, Brazilian Amazon. *Hydrobiologia* 829: 265–280.
- Araújo, M. S., D. I. Bolnick & C. A. Layman, 2011. The ecological causes of individual specialisation. *Ecology Letters* 14: 948–958.
- Armbruster, J., P. van der Sleen & N. O. Lujan, 2018. Subfamily Hypostominae – Plecos and relatives. In van der Sleen, P. & J. S. Albert (eds), *Field Guide to the Fishes of the Amazon, Orinoco, and Guianas*. Princeton University Press, Princeton: 259–285.
- Bonesi, L., P. Chanin & D. W. Macdonald, 2004. Competition between Eurasian otter *Lutra lutra* and American mink *Mustela vison* probed by niche shift. *Oikos* 106: 19–26.
- Cabral, M. M., J. Zuanon, G. E. de Mattos & F. C. Rosas, 2010. Feeding habits of giant otters *Pteronura brasiliensis* (Carnivora: Mustelidae) in the Balbina hydroelectric reservoir, Central Brazilian Amazon. *Zoologia* 27: 47–53.
- Camargo, M. & J. R. R. Ghilardi, 2009. *Entre a Terra, as Águas e os Pescadores do Médio Rio Xingu - uma abordagem ecológica*. 1st ed. Belém.

- Carter, S. K. & F. C. Rosas, 1997. Biology and conservation of the giant otter *Pteronura brasiliensis*. *Mammal Review* 27: 1–26.
- Charnov, E. L., 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology* 9: 129–136.
- Clarke, K. R. & R. N. Gorley, 2015. *PRIMER v7: User Manual/Tutorial*. Plymouth 296.
- Clarke, K. R., J. R. Tweedley & F. J. Valesini, 2014. Simple shade plots aid better long-term choices of data pre-treatment in multivariate assemblage studies. *Journal of the Marine Biological Association of the United Kingdom* 94: 1–16.
- da Silva, J. C., É. A. Gubiani, M. P. Neves & R. L. Delariva, 2017. Coexisting small fish species in lotic neotropical environments: evidence of trophic niche differentiation. *Aquatic Ecology* 51: 275–288.
- Daura-Jorge, F. G., L. L. Wedekin, V. D. Q. Piacentini & P. C. Simões-Lopes, 2005. Seasonal and daily patterns of group size, cohesion and activity of the estuarine dolphin, *Sotalia guianensis* (PJ van Bénédén)(Cetacea, Delphinidae), in southern Brazil. *Revista Brasileira de Zoologia* 22: 1014–1021.
- Dormann, C. F., B. Gruber & J. Fründ, 2008. Introducing the bipartite package: analysing ecological networks. *R News* 8: 8–11.
- dos Reis, N. R., A. L. Peracchi, W. A. Pedro & I. P. de Lima, 2011. *Mamíferos do Brasil*, 2<sup>a</sup> ed. Edur-UFRRJ, Rio de Janeiro.
- Dunne, J. A., R. J. Williams & N. D. Martinez, 2002. Food-web structure and network theory: the role of connectance and size. *Proceedings of the National Academy of Sciences* 99: 12917–12922.
- Duplaix, N., E. Evangelista & F. C. Rosas, 2015. Advances in the study of giant otter (*Pteronura brasiliensis*): ecology, behavior, and conservation: a review. *Latin American Journal of Aquatic Mammals* 10: 75–98.
- Emlen, J. M., 1966. The role of time and energy in food preference. *The American Naturalist* 100: 611–617.
- Fitzgerald, D. B., M. H. S. Perez, L. M. Sousa, A. P. Gonçalves, L. R. Py-Daniel, N. K. Lujan & J. G. Lundberg, 2018. Diversity and community structure of rapids-dwelling fishes of the Xingu River: implications for conservation amid large-scale hydroelectric development. *Biological Conservation* 222: 104–112.
- Gallagher, A. J., D. S. Shiffman, E. E. Byrnes, C. M. Hammerschlag-Peyer & N. Hammerschlag, 2017. Patterns of resource use and isotopic niche overlap among three species of sharks occurring within a protected subtropical estuary. *Aquatic Ecology* 51: 435–448.
- Garavello, J. C. & H. A. Britski, 2003. Family Anostomidae (Headstanders). In Reis, R. E., S. O. Kullander & C. J. Ferraris (eds), *Check List of the Freshwater Fishes of South and Central America*. Porto Alegre, Edipucrs: 71–84.
- Gotelli, N. J. & A. M. Ellison, 2013. *EcoSimR: null models for ecology*, version 1.00.
- Gotelli, N. J. & D. J. McCabe, 2002. Species co-occurrence: a meta-analysis of JM Diamond's assembly rules model. *Ecology* 83: 2091–2096.
- Groenendijk, J., F. Hajek, P. J. Johnson, D. W. Macdonald, J. Calvimontes, E. Staib & C. Schenck, 2014. Demography of the giant otter (*Pteronura brasiliensis*) in Manu National Park, south-eastern Peru: implications for conservation. *PLoS ONE* 9:
- Groenendijk, J., N. Duplaix, M. Marmontel, P. van Damme, C. Schenck, 2015. *Pteronura brasiliensis*. *The IUCN Red List of Threatened Species* 2015: e.T18711A21938411.
- Hernández-Romero, P. C., C. Gutiérrez-Rodríguez, C. Valdespino & D. A. Prieto-Torres, 2018. The Role of Geographical and Ecological Factors on Population Divergence of the Neotropical otter *Lontra longicaudis* (Carnivora, Mustelidae). *Evolutionary Biology* 45: 37–55.
- Instrução Normativa Interministerial 001. 3 janeiro de 2012. Diário Oficial da União.
- Junk, W. J., M. T. F. Piedade, J. Schöngart, M. Cohn-Haft, J. M. Adeney & F. Wittmann, 2011. A classification of major naturally-occurring Amazonian lowland wetlands. *Wetlands* 31: 623–640.
- Kasper, C. B., V. A. G. Bastazini, J. Salvi & H. C. Z. Grillo, 2008. Trophic ecology and the use of shelters and latrines by the Neotropical otter (*Lontra longicaudis*) in the Taquari Valley, Southern Brazil. *Iheringia. Série Zoologia* 98: 469–474.
- Kawakami, E. & G. Vazzoler, 1980. Método gráfico e estimativa de índice alimentar aplicado no estudo de alimentação de peixes. *Boletim do Instituto Oceanográfico*: 205–207.
- Krebs, C. J., 1999. *Ecological Methodology*. Benjamin Cummings, New York.
- Krpo-Četković, J., S. Subotić, S. Skorić & D. Ćirović, 2019. Diet of the Eurasian otter (*Lutra lutra*) on the River Gradac, Serbia: predation in a brown trout-dominated stream. *Aquatic Conservation: Marine and Freshwater Ecosystems* 29: 282–291.
- Leuchtenberger, C. & G. Mourão, 2009. Scent-marking of giant otter in the Southern Pantanal, Brazil. *Ethology* 115: 210–216.
- Leuchtenberger, C., L. G. R. Oliveira-Santos, W. Magnusson & G. Mourão, 2013. Space use by giant otter groups in the Brazilian Pantanal. *Journal of Mammalogy* 94: 320–330.
- Leuchtenberger, C., W. E. Magnusson & G. Mourão, 2015. Territoriality of giant otter groups in an area with seasonal flooding. *PLoS ONE* 10:
- Leuchtenberger, C., M. L. Rheingantz, C. A. Zucco, A. C. Catella, W. E. Magnusson & G. Mourão, 2020. Giant otter diet differs between habitats and from fisheries off-take in a large Neotropical floodplain. *Journal of Mammalogy* 101: 1650–1659.
- MacArthur, R. H. & E. R. Pianka, 1966. On optimal use of a patchy environment. *The American Naturalist* 100: 603–609.
- May, R. M., 1974. On the theory of niche overlap. *Theoretical Population Biology* 5: 297–332.
- Menezes, N. A., 2003. Family Acestrorhynchidae (Acestrorhynchids). In Reis, R. E., S. O. Kullander & C. J. Ferraris (eds), *Check List of the Freshwater Fishes of South and Central America*. Porto Alegre, Edipucrs: 231–233.
- Mesquita, E. M. C., R. E. A. Cruz, G. Hallwass & V. J. Isaac, 2019. Fishery parameters and population dynamics of silver croaker on the Xingu river, Brazilian Amazon. *Boletim do Instituto de Pesca* 45: 1–11.
- Muanis, M.C. & L. F. B. Oliveira, 2011. Habitat Use and Food Niche Overlap by Neotropical otter, *Lontra longicaudis*,

- and Giant otter, *Pteronura brasiliensis*, in the Pantanal Wetland, Brazil. Proceedings of Xth International Otter Colloquium, IUCN Otter Spec. Group Bull 28A: 76–85.
- Oyakawa, O. T. & G. M. T. Mattox, 2018. Family Erythrinidae – Wolf-fishes and yarrows. In van der Sleen, P. & J. S. Albert (eds), Field Guide to the Fishes of the Amazon, Orinoco, and Guianas. Princeton University Press, Princeton: 156–158.
- Papastamatiou, Y. P., B. M. Wetherbee, C. G. Lowe & G. L. Crow, 2006. Distribution and diet of four species of carcharhinid shark in the Hawaiian Islands: evidence for resource partitioning and competitive exclusion. Marine Ecology Progress Series 320: 239–251.
- Pardini, R., 1998. Feeding ecology of the neotropical river otter *Lontra longicaudis* in an Atlantic Forest stream, south-eastern Brazil. Journal of Zoology 245: 385–391.
- Pianka, E. R., 1974. Niche overlap and diffuse competition. Proceedings of the National Academy of Sciences 71: 2141–2145.
- Quintela, F. M., L. G. S. Artioli & R. A. Porciuncula, 2012. Diet of *Lontra longicaudis* (Olfers, 1818) (Carnivora: Mustelidae) in three limnic systems in southern Rio Grande do Sul state, Brazil. Brazilian Archives of Biology and Technology 55: 877–886.
- R Development Core Team, 2019. R: A Language and Environment for Statistical Computing.
- Rheingantz, M. L. & C. S. Trinca, 2015. *Lontra longicaudis*. The IUCN Red List of Threatened Species 2015: e.T12304A21937379.
- Rheingantz, M. L., H. F. Waldemarin, L. Rodrigues & T. P. Moulton, 2011. Seasonal and spatial differences in feeding habits of the Neotropical otter *Lontra longicaudis* (Carnivora: Mustelidae) in a coastal catchment of south-eastern Brazil. Zoologia. Curitiba 28: 37–44.
- Rheingantz, M. L., J. F. S. de Menezes & B. de Thoisy, 2014. Defining Neotropical otter *Lontra longicaudis* distribution, conservation priorities and ecological frontiers. Tropical Conservation Science 7: 214–229.
- Rheingantz, M. L., V. M. Santiago-Plata & C. S. Trinca, 2017. The Neotropical otter *Lontra longicaudis*: a comprehensive update on the current knowledge and conservation status of this semiaquatic carnivore. Mammal Review 47: 291–305.
- Sabaj Pérez, M. H., 2015. Where the Xingu bends and will soon break. American Scientist 103: 395–397.
- Schirmer, A., J. Hoffmann, J. A. Eccard & M. Dammhahn, 2020. My niche: individual spatial niche specialization affects within-and between-species interactions. Proceedings of the Royal Society B 287: 20192211.
- Schofield, K. A., L. C. Alexander, C. E. Ridley, M. K. Vanderhoof, K. M. Fritz, B. C. Autrey, J. E. DeMeester, W. G. Kepner, C. R. Lane, S. G. Leibowitz & A. I. Pollard, 2018. Biota connect aquatic habitats throughout freshwater ecosystem mosaics. JAWRA Journal of the American Water Resources Association 54: 372–399.
- Sidlauskas, B. & J. L. O. Birindelli, 2018. Family Anostomidae – Toothed Headstanders. In van der Sleen, P. & J. S. Albert (eds), Field Guide to the Fishes of the Amazon, Orinoco, and Guianas. Princeton University Press, Princeton: 82–89.
- Sih, A. & B. Christensen, 2001. Optimal diet theory: when does it work, and when and why does it fail? Animal Behaviour 61: 379–390.
- Silva, R. E., F. C. W. Rosas & J. Zuanon, 2013. Feeding ecology of the giant otter (*Pteronura brasiliensis*) and the Neotropical otter (*Lontra longicaudis*) in Jaú National Park, Amazon, Brazil. Journal of Natural History 48: 465–479.
- Souza, K. S., V. A. Bastazini & E. P. Colares, 2013. Feeding ecology of the Neotropical otter *Lontra longicaudis* in the Lower Arroio Grande River, southern Brazil. Anais da Academia Brasileira de Ciências 85: 285–294.
- Strauss, R. E., 1979. Reliability Estimates for Ivlev's Electivity Index, the Forage Ratio, and a Proposed Linear Index of Food Selection. Transactions of the American Fisheries Society 108: 344–352.
- Thompson, R. M., U. Brose, J. A. Dunne, R. O. Hall Jr., S. Hladyz, R. L. Kitching, N. D. Martinez, H. Rantala, T. N. Romanuk, D. B. Stouffer & J. M. Tylianakis, 2012. Food webs: reconciling the structure and function of biodiversity. Trends in Ecology & Evolution 27: 689–697.
- Trigila, A. P., J. J. Gómez, M. H. Cassini & J. I. Túnez, 2015. Genetic diversity in the Neotropical river otter, *Lontra longicaudis* (Mammalia, Mustelidae), in the Lower Delta of Paraná River, Argentina and its relation with habitat suitability. Hydrobiologia 768: 287–298.
- Vermaat, J. E., J. A. Dunne & A. J. Gilbert, 2009. Major dimensions in food-web structure properties. Ecology 90: 278–282.
- Wiens, J. J., D. D. Ackerly, A. P. Allen, B. L. Anacker, L. B. Buckley, H. V. Cornell, et al., 2010. Niche conservatism as an emerging principle in ecology and conservation biology. Ecology Letters 13: 1310–1324.

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.