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Giant otter diet differs between habitats and from fisheries offtake in a large Neotropical floodplain

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Giant otters *Pteronura brasiliensis* are semiaquatic mammals that mainly eat fish, the abundance of which is affected by seasonal flooding and habitat structure. The piscivorous habits of giant otters lead to negative human perception and conflicts with fisheries. We compared giant otter feeding habits between seasons and habitats in the Southern Pantanal, Brazil, by analyzing feces collected between September 2008 and June 2011.We investigated whether habitat and season affected *P. brasiliensis* diet composition and prey size. We calculated the frequency of occurrence, relative frequency, and overlap of fish species eaten by giant otters and caught by fishermen. The giant otters had a more diverse assemblage of fish prey than the offtake in the fisheries. We did not find strong seasonality in otter diets, but diet composition and prey size differed between rivers and lakes. The giant otter diet had higher overlap with the offtake of sport than with professional fishermen. Although the otters' piscivorous diet often leads to negative perceptions by humans, the low overlap between otter diet and species taken in local fisheries suggests that otters have little effect on the commercial fishery. These results indicate that educational programs could be used to reduce perceived conflict between giant otters and fishermen.

Key words: diet overlap, human–wildlife conflict, opportunistic predator, prey size, *Pteronura brasiliensis*, seasonality

As ariranhas *Pteronura brasiliensis* são mamíferos semiaquáticos que comem principalmente peixes, cuja abundância é afetada pelas inundações sazonais e pela estrutura do habitat. Seus hábitos piscívoros levam à percepção humana negativa e conflitos com pescadores. Comparamos os hábitos alimentares de ariranhas entre estações do ano e habitats no sul do Pantanal, Brasil, analisando amostras fecais coletadas entre setembro de 2008 e junho de 2011. Investigamos se habitat e estação afetam a composição da dieta e o tamanho das presas de *P. brasiliensis*. Calculamos a frequência de ocorrência, frequência relativa e a sobreposição das espécies de peixes consumidas por ariranhas e os peixes capturados por pescadores. As ariranhas apresentaram um conjunto de presas mais diversificado do que os peixes capturados nas pescarias. Não encontramos uma forte sazonalidade na dieta de ariranhas, mas a composição da dieta e o tamanho das presas diferiram entre rios e lagos. A dieta das ariranhas teve maior sobreposição com os pescadores esportivos do que com os profissionais. Embora a dieta piscívora das ariranhas frequentemente leve à percepção negativa pelos seres humanos, a baixa sobreposição entre a dieta das ariranhas e as espécies capturadas na pesca local sugere que ariranhas tem um baixo efeito negativo na pesca comercial. Estes resultados indicam que programas educativos poderiam ser usados para reduzir o conflito percebido entre ariranhas e pescadores.

Palavras-chave: conflito entre humano e vida selvagem, predador oportunista, *Pteronura brasiliensis*, sazonalidade, sobreposição de dieta, tamanho da presa

For species with high metabolic rates, such as mammalian carnivores, spatial and temporal variation in food availability may lead predators to become more opportunistic under low density of preferred prey (Ben-David et al. 1997; Day et al. 2015). Food availability also may affect social organization and space use by species with specialized diets (Gittleman and Harvey 1982; Macdonald 1983).

Otters are semiaquatic carnivores that appear to modify their diet according to prey availability (Clavero et al. 2003; Anoop et al. 2005; Rheingantz et al. 2017). Giant otters *Pteronura brasiliensis* are one of the most social otters, living in groups that defend territories along water bodies in seasonally flooded areas (Leuchtenberger et al. 2015). Although living in areas subject to seasonal flooding, and consequently with different resource availability and environmental conditions, groups maintain social cohesion across seasons (Leuchtenberger and Mourão 2008), increasing their home range during the wet season (Leuchtenberger et al. 2013).

Although foraging in groups, giant otters usually capture prey individually and do not share their prey (Duplaix 1980; Rosas et al. 1999; but see also Davenport 2010). Groups seem to concentrate foraging efforts near the riverbank and under aquatic vegetation, or in shallow and lentic water bodies. The species is considered as an opportunist predator (Rosas et al. 1999; Cabral et al. 2010; Rosas-Ribeiro et al. 2012), although studies of giant otter diet have not measured prey availability.

Flooding is known to affect the behavior and distribution of fish species across flooded areas (Lower-McConnell 1999), which spread out during the wet season. This is expected to affect the behavior of predators, such as giant otters, with respect to fish. Territoriality also may affect access to better foraging sites, particularly under high population density. In the Southern Pantanal, where the giant otter population may have reached carrying capacity, groups living in marginal environments have been reported taking unusual prey, such as caiman (*Caiman crocodilus yacare*—Ribas et al. 2012), which may be a response to resource scarcity or intraspecific competition. The suitability of marginal habitats in the Southern Pantanal for giant otter groups still is poorly known, but an increase in intake of small benthic fishes and nonfish prey suggests that these habitats are suboptimal. Living in marginal habitats leads to an increase in disease and stress, and may result in death of individuals and disintegration of groups (Leuchtenberger et al. 2015). The effects of season and habitat on diets of giant otters inhabiting floodplains are poorly known, especially in areas with high otter population density, where some groups are forced to inhabit suboptimal locations.

In addition, the piscivorous habit of giant otters often leads to negative perceptions and conflicts with fishermen, who as a result become a threat to some populations (Zucco and Tomás 2004; Recharte et al. 2008; Rosas-Ribeiro et al. 2012; Lima et al. 2014). The killing of 64 giant otters by the Kanamari indigenous people due to their perception that the species was overfishing the river-turtle population is an example of how human–otter conflict can deplete small populations (Leuchtenberger et al. 2018). In a Sustainable Reserve in the Brazilian Amazon, traditional people have solicited permission to manage giant otters due to their interference with fishing activities (Dalponte and Oliveira 2015). In 2017, members of a giant otter group were killed by fishermen in the Pantanal and, according to locals, killings occurs frequently during the fishing season (Leuchtenberger et al. 2018). Although fishermen see giant otters as competitors, little is known about the extent of overlap between the fish composition of giant otter diets and catches of fisheries in areas of co-occurrence (Rosas-Ribeiro et al. 2012) and such information could help to plan strategies to manage and reduce conflicts. As the Brazilian Pantanal receives ~17,500 sport and artisanal-professional fishermen during the fishing season (March to October) every year (Catella et al. 2017), the potential for human conflicts with giant otters is large. The term artisanal-professional is used to designate the professional fishermen of the Pantanal because in this region, fisheries regulation allows only the use of gear based on hook and line (use of nets and trawls were banned in the 1990s).

We analyzed the diet of otters from different otter groups in the Southern Pantanal based on fecal samples and investigated whether habitat and season affect diet composition and prey size, and compared otter diets to the composition of fish caught by sport and professional fishermen in the same study site. We initiated the study with three hypotheses: (1) prey size and diet composition of giant otters would differ between habitat (river or lake) and season (flooding or low-water); (2) the diet of giant otter groups would be more diverse than sport and professional fisheries, with low overlap among the groups; and (3) assuming that giant otters are opportunist predators, overlap between giant otter diet and sport fisheries would be larger than the overlap between otter diets and professional fisheries, as the latter are more selective than the sport fishermen.

Materials and Methods

Ethical statements.—The giant otter is an endangered species (Groenendijk et al. 2015) that is vulnerable to disturbance, especially in dens and in the latrines where they defecate. Collection of fecal samples therefore was carried out with caution by a single researcher who remained on the latrine site the minimum amount of time necessary to collect feces with minor ancillary trampling. Monitoring and observation of groups was undertaken to determine which group used each latrine. All monitoring procedures were carried out carefully to avoid unnecessary changes in otter behavior and authorized under license No. 12794/4 of the Brazilian Institute of Environment and Renewable Natural Resources (ICMBio). Fish capture for preparing a fish-bone collection for diet analysis was authorized under license No. 008/2010 of the Environmental Institute of Mato Grosso do Sul (IMASUL). The study followed ASM guidelines (Sikes et al. 2016) and was approved by the Ethics Committee of the National Institute of Amazonian Research (No. 028/2013).

Data collection and fecal analysis.—The study was conducted in the Southern Pantanal of Brazil. The Pantanal is a large wetland that covers about 160,000 km^2 in the center of South America. Most of the annual precipitation of 1,200 mm occurs between November and March, causing inundation of about 80% of the region (Hamilton et al. 1996).

Between September 2008 and June 2011, we collected fecal samples from latrines found along stretches of the Negro, Miranda, and Vermelho, Rivers (called "river" samples), totaling 135 km of water bodies, and some lakes along the Miranda River and artificial ponds along the Estrada Parque Road (MS-184) and the BR-262 Highway (called "lake" samples; Fig. 1). Samples from lakes and artificial ponds were merged for analysis because their prey assemblages are regulated by similar ecological constraints. These lakes receive water from rivers only through shallow channels when the river levels are at their highest, which limits the size and variety of fishes that can populate the lake. When the lakes become isolated from the river, predators reduce fish abundance as the dry season advances. Variation in river level was measured every day at a fixed station on the Miranda River, located at 19°34′37.97″S, 57°01′7.34″W, 92 m. Flooding tended to be abrupt, and the transition between seasons occurred within a few weeks. During the study period, the level of the Miranda River varied from 126 to 481 cm and the rivers overflowed at heights > 300 cm. Based on this, we recognized three low-water seasons (June–December 2008; June–December 2009; and July 2010–January 2011) and three flooding seasons (January–May 2009; January–June 2010; and February–June 2011).

We searched for fresh latrines of giant otters in most of the study area using a motorboat powered by a 15-hp motor, but some water bodies beside roads only could be accessed by land. Searching effort varied among study sites. The Miranda and Vermelho Rivers were surveyed monthly in campaigns of 7–10 days, totaling 193 survey days. We surveyed the Negro River in four campaigns also of 7–10 days, totaling 34 survey days. The Estrada Parque Road (unpaved) and BR-262 Highway were surveyed opportunistically, resulting in 81 survey days (74 days during flooding season and 7 days during dry seasons). At least 106 individuals from 17 giant otter groups used the area at that time.

While defecating in communal latrines, giant otters scatter the soil, mixing the feces of several individuals of the group (Leuchtenberger and Mourão 2009), which made it impractical to identify feces of different individuals. We collected fresh fecal material from 136 active latrines. However, some groups had material taken from more than one latrine in a given season and habitat. In these instances, we merged the material collected from latrines of a same group in the same habitat/season, to improve the independence of the samples. This procedure resulted in 26 samples by groups/habitat/season. We took the geographical position of latrines with a GPS (Garmin Etrex 20, Garmin International, Inc., Olathe, Kansas), and fecal samples were stored in labeled plastic bags.

We washed the samples under running water over a fine mesh (1-mm) sieve and left them to dry in an oven at 30°C for 3 days. After drying, we separated the fecal remains into large taxonomic groups (fish, crustaceans, reptiles, mammals, mollusks, and insects). After this preliminary identification, we attempted to identify the fragments of each group to the lowest possible taxonomic level as in similar studies (e.g., Rosas et al. 1999). We inferred the minimum number of prey individuals in each sample from the number of matched otoliths, eye lenses, maxilla, premaxilla, and dentary bones and/or pectoral- and dorsal-fin structures that allowed individuals to be counted (Romero et al. 2012). Comparisons of these hard structures with a reference collection allowed prey identification and prey-size estimation.

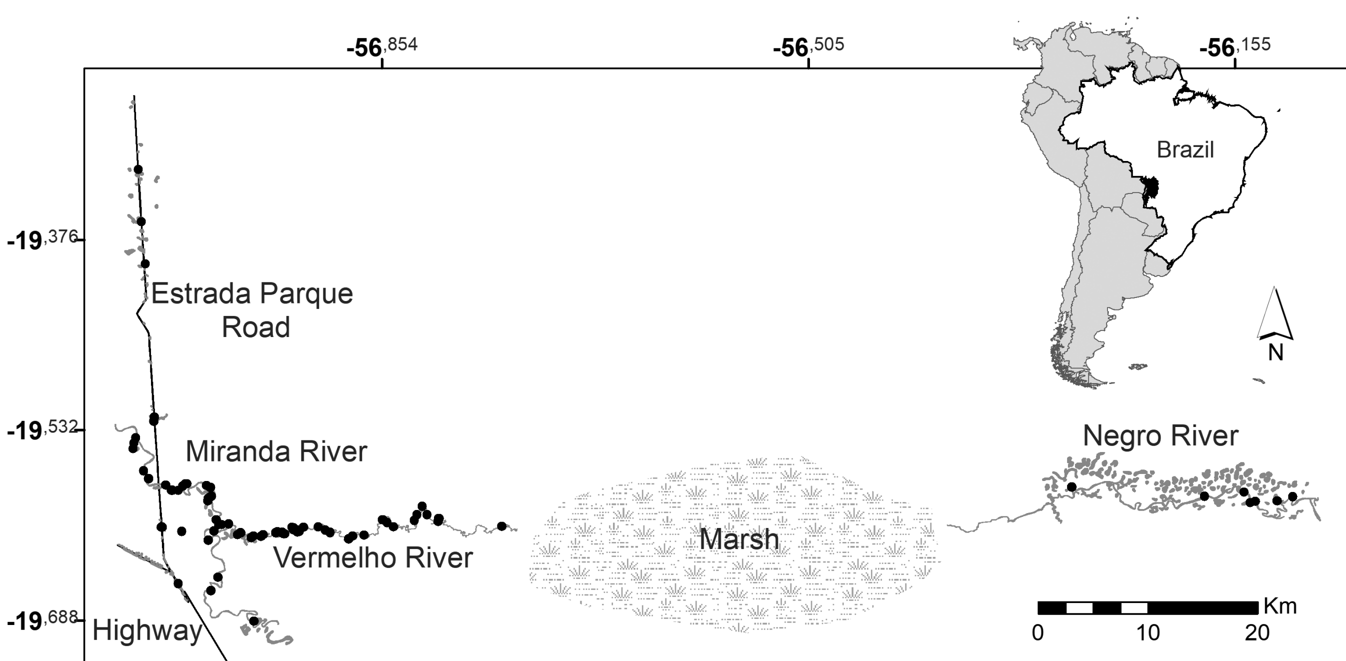

Fig. 1.—Map of the study area, showing the sites where fecal samples (black dots) of giant otters were collected for diet analysis in the Southern Pantanal, between September 2008 and June 2011.

To prepare a fish-bone collection, we collected at least six individuals of different sizes from each of the 12 most frequent fish species that we caught in the study area. These fish were captured using cast and gill nets and frozen soon after capture. We measured scales of each fish species from specimens of different sizes with a digital slide caliper (limit of reading 0.01 mm). We boiled each specimen to extract the hard body structures to measure and include in the collection. The reference collection was deposited in the Scientific Collection of Vertebrates of Embrapa Pantanal. We used species-specific linear regressions (see Supplementary Data SD1) to estimate prey size based on size of the hard prey structures found in the fecal samples, a technique frequently used in studies of other otter species (Wise 1980; Taastrøm and Jacobsen 1999; Anoop and Hussain 2005).

Fishing data.—Data on fish caught by professional and sport fishermen were obtained from the annual fisheries control system that monitors fishing in Mato Grosso do Sul state (Catella et al. 2017). The acquisition of fishing data is carried out during inspection activities of the Environmental Police and the State Environmental Agency (IMASUL) that controls fishing activities around 15 fishing sites in Mato Grosso do Sul state. Fish caught by professional and sport fishermen in each fishery campaign were sorted by species and weighed by Environmental Police officers, who filled in the data for the transport licenses given to the fishermen. Each fisheries campaign could take one or more consecutive days and involve one or more fishermen. Because there are minimum length limits for many fish species, the officers also often measure the fish. Most of the officers filled out the datasheets with data grouped by species, as individual biometric information is not required by the State Fisheries Control System. However, some meticulous officers did annotate the length and weight of every fish. We had access to the original forms filled out by the officers and searched for those with detailed information on the fish caught. From this subset, we used information on 20 professional and 20 sport fishermen (10 in low-water season and 10 in flooding season, for each class of fisheries) that had fished in the study area (i.e., Miranda River or Buraco das Piranhas site) during the same period we collected fecal samples (September 2008 to June 2011). Sometimes, the number of fish of noncontrolled species was not included in the datasheet, although the pooled weight for these species was registered. In these cases, we used the pooled weight to estimate the number of specimens of a given species caught in that fishery, using the equations that report weight and numbers of individuals for different species of fish, as supplied by Catella and Albuquerque (2010).

Statistical analyses.—All statistical analyses were carried out using R 3.6.3 Software (R Development Core Team, 2020). We calculated the frequency of occurrence (FO) as the number of fecal samples with a certain prey species relative to the total number of samples examined. "Sample" here means the merged fecal material taken from latrines of each group found in a given habitat type (river or lake) and given season (flooding or low-water).

To express the diet composition of giant otter groups in each season and habitat, we calculated the relative frequency (RF) of prey species, as the number of each prey in the sample in relation to the total prey abundance in the sample (see Bojarska and Selva 2012).

We used a two-way ANOVA with repeated measures to test for differences in size of giant otter prey between habitats and seasons, repeating localities between seasons. For this analysis, we excluded one lake, located beside the BR-262 Highway, which was not sampled during the flood season. We then used a Permutational Multivariate Analysis of Variance (PERMANOVA) with the Bray–Curtis dissimilarity distance, to investigate whether habitat, season, and their interaction affected the composition of giant otters' diets. We ran the PERMANOVA (Anderson 2001) using the *adonis* function in the vegan 2.5-1 package (Oksanen et al. 2018) with 5,000 randomizations.

We express the composition of fisheries catches by FO and RF of fish species caught, as was done for giant otter diet. For this analysis, we considered each fishery campaign as recorded by the Environmental Police to constitute an independent sample. We calculated FOs and RFs for each season, but just for the river habitat, as lakes are rarely used for fishing in that area.

We estimated the expected asymptotic number of taxa consumed by giant otters and caught by fishermen through the bootstrap method, using the function *specpool*, and examined graphically the number of taxa in samples using the function *specnumber*, both from the vegan 2.5-1 package (Oksanen et al. 2018). We analyzed the effects of source (giant otter feces, sport fisheries, or professional fisheries) and season (flooding or low-water) on the fish composition of samples, with a second PERMANOVA model, also using the Bray–Curtis distance and with 5,000 randomizations. To evaluate the overlap between the diet of giant otters and the fish species taken by human fisheries in the different seasons in riverine habitat we used the Morisita–Horn index (divo 3.4.4 package—Sadee et al. 2017).

Results

Giant otter diet.—Fish were found in all fecal material sampled (n = 136 fecal material collections belonging to 17 otter groups or 26 groups/habitat/season), followed by Gastropoda (n = 27; 20% of the fecal samples) and Malacostraca (n = 15; 11%). Insects, reptiles, and mammals, occurred rarely (6%, 6%, and 0.7%, of the latrines, respectively). Most fish in samples were of the order Characiformes, with *Hoplias* sp. (Erithrinidae) being the most frequent food type in both seasons and habitats (FO = 100% in the three cases; Table 1), followed by *Serrasalmus* sp. (Serrasalmidae; hereafter, "piranhas"), which was more frequent during the flooding season (FO = 78.6%). *Hoplias* was the most important single prey type in terms of RF (Table 2) in both seasons and in both habitats, always accounting for more than 20% of the prey recorded. Piranhas were more frequent in samples from rivers (RF = 20.8%) than lakes (2.9%). *Piaractus* sp. (Serrasalmidae) was more frequent during the flooding

Table 1.—Corumbá, Mato Grosso do Sul—Frequency of occurrence (FO) of prey found in 136 latrines of 17 giant otter groups (*Pteronura brasiliensis*) and of fish taken by sport (Sport) and professional (Prof) fishermen in the southern Pantanal, Brazil between September 2008 and June 2011. We evaluated the diet of giant otter groups inhabiting rivers and lakes, during flooding and low-water seasons. Fisheries occurred only in rivers.

	Season						Habitat			
	Flooding			Low-water			Lake		River	
	Otter	Sport	Prof	Otter	Sport	Prof	Otter	Otter	Sport	Prof
Characiformes	100	90	60	100	100	90	100	100	95	75
Acestrorhyncus	7.1	0	0	7.1	0	0	0	9.1	0	0
Astyanax	28.6	0	0	21.4	0	0	16.7	27.3	0	0
Brycon	28.6	10	0	35.7	60	30	0	40.9	35	15
Hoplias	100	0	0	100	0	0	100	100	0	0
Leporinus	35.7	10	0	42.9	20	20	33.3	40.9	15	10
Piaractus	64.3	50	40	50	80	60	33.3	63.9	65	50
Prochilodus	35.7	0	0	35.7	30	0	16.7	40.9	15	0
Salminus	42.9	0	30	50	20	50	0	59.1	10	40
Serrasalmus	78.6	80	20	57.1	40	10	33.3	77.3	60	15
Triportheus	50	0	0	21.4	0	0	0	13.6	0	0
Cyprinodontiformes	7.1	0	0	14.3	0	0	50	0	0	0
Poeciliidae	7.1	0	0	14.3	0	0	50	0	0	0
Perciformes	57.1	20	0	92.9	0	0	83.3	72.7	10	0
Cichlidae[a]	57.1	0	0	92.9	0	0	83.3	72.7	0	0
Cichla	0	20	0	0	0	0	0	0	10	0
Siluriformes	78.6	80	100	71.4	90	90	100	68.2	85	95
Ageneiosus	0	40	20	0	10	0	0	0	25	10
Callichthys	71.4	0	0	50	0	0	83.3	54.5	0	0
Hemisorubim	0	10	0	0	60	0	0	0	20	0
Hypostomus	21.4	0	0	21.4	0	0	16.7	22.7	0	0
Pterygoplichthys	42.9	0	0	50	0	0	66.7	40.9	0	0
Pimelodus	28.6	0	0	42.9	0	0	33.3	36.4	0	0
Pinirampus	0	20	30	0	10	10	0	0	15	20
Platydoras	28.6	0	0	28.6	0	0	0	36.4	0	0
Pseudoplastystoma	14.3	70	100	14.3	70	80	0	18.2	70	90
Sorubim	0	0	0	0	40	0	0	0	20	0
Zungaro	0	0	30	0	30	40	0	0	15	35
Reptilia	21.4			28.6			16.7	27.3		
Caiman	0			7.1			16.7	0		
Salvator	21.4			21.4			0	27.3		
Mammalia	0			1.4			0	0.9		
Nectomys	0			1.4			0	0.9		
Insecta	21.4			28.6			16.7	27.3		
Gastropoda	57.1			50			100	40.9		
Ampularidae	57.1			50			100	40.9		
Malacostraca	50			21.4			66.7	27.3		
Trichodactylus	50			21.4			66.7	27.3		

[a] Except *Cichla*.

season (FO = 64.3%) and its RF was higher in samples from riverine habitats (RF = 7.5%) than in samples collected in lakes (RF = 2.1%). Catfishes (Siluriformes) were found more often in lake samples than in river samples (FO = 100% and 68.2%, respectively), probably due to the high frequency of small benthic catfishes, such as *Callichthys* (Callichthyidae; FO = 83.3) and armored catfishes, such as *Pterygoplichthys* (Loricariidae; FO = 66.7%). Ampulariidae (Gastropoda) was the most frequent nonfish item in lake samples (FO = 100%, RF = 15.8%). *Caiman* (Alligatoridae) remains were found only in samples collected in lakes (FO = 16.7%) and during the low-water season (FO = 7.1%) and accounted for a small proportion of the prey (RF ≤ 0.8% in both cases).

Influence of habitat and season on giant otter diet.—Prey size differed between habitats ($F_{1,2} = 74.441$, $P = 0.013$), but not between seasons ($F_{1,2} = 2.993$, $P = 0.226$; Fig. 2). Giant otter groups inhabiting rivers consumed larger fish ($\bar{X} = 197.6$ mm; $SD = 41.6$ mm, $n = 567$; Fig. 2) than those from lakes ($\bar{X} = 147.3$ mm; $SD = 42.8$ mm, $n = 162$).

Diet composition of giant otters found in lakes differed from the diet of those from rivers ($F_{1,24} = 2.931$, $P = 0.014$, $r^2_{partial} = 0.10$); but neither season nor the interaction term affected the diet composition ($F_{1,24} = 1.605$, $P = 0.126$ and $F_{1,24} = 0.238$, $P = 0.975$, respectively).

Overlap between giant otter diet and fisheries offtake.—The bootstrap analysis indicated an expected asymptotic number between 23 and 24 taxa ($SE = 0.7$) in the diet of the giant otters, while the asymptotic number of fish taxa registered in sport and professional fisheries samples from the study site ranged from 13 to 14 ($SE = 0.7$) and 8 to 9 ($SE = 0.6$), respectively, suggesting that giant otters take more diverse prey than do fishermen (Fig. 3). Professional

Table 2.—Relative frequency (RF) of prey found in 136 latrines of 17 giant otter groups (*Pteronura brasiliensis*) and from fish taken by 20 sport (Sport) and 20 professional (Prof) fishermen tabulated by season (flooding or low-water) or habitat (lake or river) in the southern Pantanal, Brazil between September 2008 and June 2011.

	Season						Habitat			
	Flooding			Low-water			Lake		River	
	Otter	Sport	Prof	Otter	Sport	Prof	Otter	Otter	Sport	Prof
Characiformes	55	91.3	24.2	67.8	83.2	37.7	36.1	70.7	86	29.5
Acestrorhyncus	0.2	0	0	0.5	0	0	0	0.5	0	0
Astyanax	1.3	0	0	0.7	0	0	0.4	1.2	0	0
Brycon	2.6	3.4	0	1.6	20.4	5.5	0	2.9	14.9	2.3
Hoplias	20.6	0	0	36	0	0	27.8	28.5	0	0
Leporinus	3.4	3.9	0	3.6	21.2	4.8	2.5	3.8	15.6	1.9
Piaractus	8.5	14.2	13.9	3.6	13.1	21.1	2.1	7.5	13.5	16.7
Prochilodus	2	0	0	1.1	19	0	0.4	2	12.8	0
Salminus	3.1	0	1.4	2	1	3.7	0	3.5	0.7	2.3
Serrasalmus	13.2	69.8	8.9	18.7	8.5	2.2	2.9	20.8	28.5	6.3
Triportheus	0.4	0	0	0.2	0	0	0	0.5	0	0
Cyprinodontiformes	1.3			0.9			4.2	0		
Poeciliidae	1.3			0.9			4.2	0		
Perciformes	7.4	0.9	0	8.1	0	0	8.7	7.4	0.3	0
Cichlidae[a]	7.4	0	0	8.1	0	0	8.7	7.4		
Cichla	0	0.9	0	0	0	0	0	0	0.3	0
Siluriformes	20.1	7.8	75.8	17.7	16.8	62.2	31.1	14.3	13.7	70.6
Ageneiosus	0	2.6	5.2	0	0.4	0	0	0	1.1	3.2
Callichthys	5.9	0	0	6.3	0	0	10	4.8	0	0
Hemisorubim	0	0.4	0	0	4.2	0	0	0	2.9	0
Hypostomus	2.9	0	0	1.1	0	0	4.1	1.2	0	0
Pimelodus	2	0	0	3.4	0	0	4.6	2	0	0
Pinirampus	0	0.9	2.8	0	1.9	0.4	0	0	1.4	1.9
Platydoras	1.6	0	0	1.4	0	0	0	2	0	0
Pseudoplastystoma	0.4	3.9	65.9	0.5	4.4	57.4	0	0.6	4.2	62.6
Pterygoplichthys	7.2	0	0	4.9	0	0	12.4	3.7	0	0
Sorubim	0	0	0	0	4.2	0	0	0	2.8	0
Zungaro	0	0	1.9	0	1.9	4.4	0	0	1.3	2.9
Reptilia	0.7			1.2			0.8	0.9		
Caiman	0			0.5			0.8	0		
Salvator	0.7			0.7			0	0.9		
Mammalia	0			0.2			0	0.2		
Nectomys	0			0.2			0	0.2		
Insecta	0.7			0.9			0	0.9		
Gastropoda	11.6			2.5			15.8	3.8		
Ampularidae	11.6			2.5			15.8	3.8		
Malacostraca	2.7			0.9			2.9	1.4		
Trichodactylus	2.7			0.9			2.9	1.4		

[a] Except *Cichla*.

fishermen mainly took large and economically valuable fish, such as the large catfishes, and the sport fishery was concentrated on the fish that were more available and/or easier-to-catch, such as "piranhas" during the flooding season or *Leporinus* (Characiformes: Anostomidae) and *Brycon* (Characiformes: Characidae) during the low-water season (Table 2). The PERMANOVA indicated that the assemblage of fish consumed by the otters differed from the assemblage taken by fishermen ($F_{2,62} = 22.335$, $r^2_{partial} = 0.39$, $P < 0.001$). Also, season ($F_{1,62} = 2.574$, $P = 0.022$) and the interaction between source and season ($F_{2,62} = 1.925$, $P = 0.036$) were significant, but explained little of the model variation ($r^2_{partial} = 0.02$ and $r^2_{partial} = 0.04$, respectively).

Overlap between professional fisheries and giant otter diets were low (≤ 9.7%) in any combination of seasons (Table 3). In rivers, the overlap between the sport fisheries and giant otter diet (49.2%) was larger than between sport and professional fisheries (23.6%) and between otter diet and professional fisheries (9.1%). The average overlap between the sport fisheries during the flooding season and the diet of giant otter groups was larger than within sport fisheries, regardless of whether the otters' diet was assessed during the flooding season (34.6%) or during the low-water season (38.1%). The catch from professional fisheries largely was independent of the season, with about 96% of mean overlap between assemblages taken in different seasons (Table 3), reflecting the high selectivity by professional fishermen for the more valuable fishes, especially the large and valuable catfish *Pseudoplatystoma* (Pimelodidae). The giant otter diet also exhibited a large overlap between seasons (80.3%), but unlike the catch of professional fishermen, the most common prey were the relatively easy-to-catch *Hoplias* and the very abundant "piranhas." They also ate a variety of other fish species. The average overlap between the catches of sport fisheries undertaken in different seasons was relatively small (26.2%).

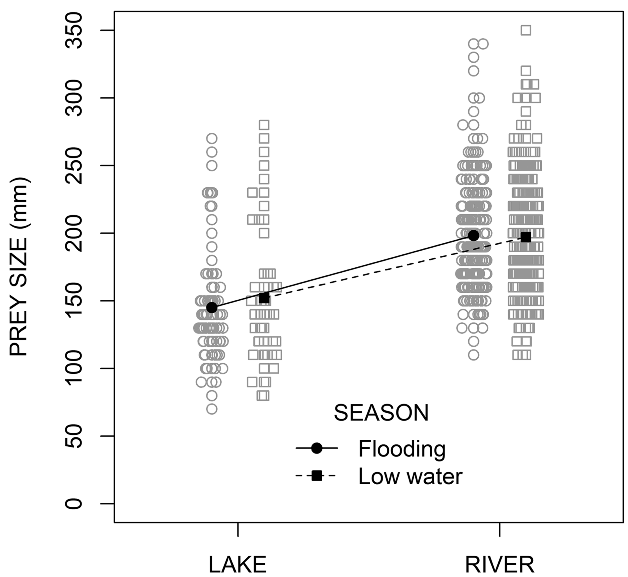

Fig. 2.—Distribution of fish sizes (mm) consumed by giant otter groups as a function of habitat and season in water bodies in the southern Pantanal, from September 2008 to June 2011.

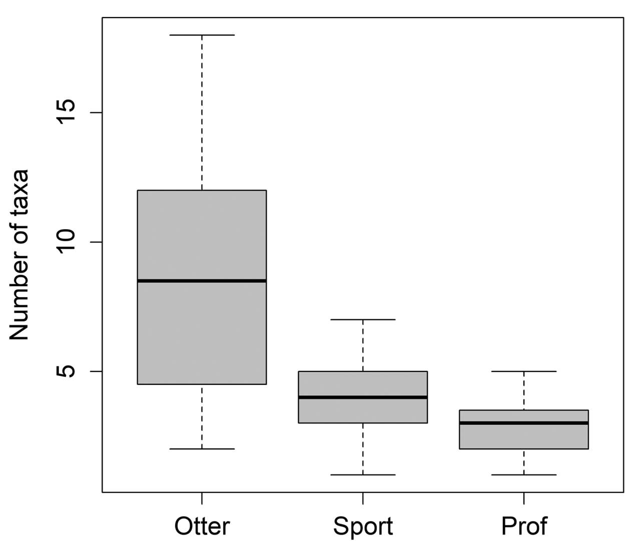

Fig. 3.—Boxplot presenting the number of prey taxa consumed by giant otter (Otter) and number of fish taxa caught by sport (Sport) and professional fisheries (Prof) in the southern Pantanal, from September 2008 to June 2011.

Discussion

Giant otters' diet across habitat and seasons.—Giant otters in the Pantanal principally consume medium to large fish, as has been reported for studies in other areas (Duplaix 1980; Schweizer 1992; Rosas et al. 1999; Cabral et al. 2010; Rosas-Ribeiro et al. 2012; Silva et al. 2014). Otter groups inhabiting marginal habitat, such as the shallow and/or temporary lakes, took small fishes or other alternative preys. Shallow, lentic, and oxygen-limited environments, such as most isolated lakes in the Pantanal, represent patches with different prey composition and favor the occurrence of small species that are sedentary or

Table 3.—Percent mean overlap estimated with Morisita–Horn index (Krebs 1999) among catch of sport fishermen (Sport), catch of professional fishermen (Prof), and giant otter diet (Otter) during the low-water (lw) and flooding (fl) seasons in the southern Pantanal, from September 2008 to June 2011.

	Sport (lw)	Sport (fl)	Prof (lw)	Prof (fl)	Otter (lw)
Sport (fl)	26.5				
Prof (lw)	26.3	14.3			
Prof (fl)	16.4	19.9	95.8		
Otter (lw)	17.0	38.7	4.4	6.1	
Otter (fl)	27.9	34.6	9.7	8.0	80.3

have low mobility (Súarez et al. 2004; Baginski et al. 2007; Fernandes et al. 2010). The composition of fecal samples reflected this, with the high occurrence of small Perciformes and Siluriformes in lake samples, orders that are known to be abundant in such environments (Lower-McConnell 1999), and other nonfish prey, such as snails and crabs, that were rare in the diet of otters inhabiting rivers.

Seasonal inundation is the key factor for the maintenance of Pantanal productivity (Harris et al. 2005). Flooding affects the activity and availability of fish and the aquatic community (Lower-McConnell 1999; Fernandes et al. 2010), which also affects the behavior and diet of piscivorous predators (Lower-McConnell 1999). However, we did not detect significant differences in giant otter diet composition between seasons. This may reflect some level of prey selection by the giant otter, which seem to spend more time traveling longer distances during the flooding season, probably following their preferred prey into flooded and shallow areas (Duplaix 1980). This increase in foraging effort also results in faster daily locomotion and larger home ranges during this period (Leuchtenberger et al. 2013).

Seasonality also affects the suitability of marginal lakes, which become isolated during the dry season, attracting piscivores such as birds, caimans, and giant otters (Ribas et al. 2012). However, as the dry season advances, the concentration of predators increases, and prey becomes depleted. Residence of giant otter groups in such habitats is uncommon, but it was observed during our study. Although giant otters usually prefer mid- to large-sized fish (Duplaix 1980; Silva et al. 2014), for groups that inhabited artificial lakes opportunism is vital and they will need to have a more varied diet and to consume smaller fishes. Considering the high metabolic requirements of the species, prey consumed by giant otters in marginal and artificial lakes probably represent the largest or most abundant species available in that habitat. These results reinforce the feeding plasticity of opportunistic predators under extreme conditions.

Long-term monitoring of the studied populations suggests that the presence of giant otters in artificial lakes is a response to high population density, which seems to have reached the carrying capacity in the study area at least 10 years ago (Leuchtenberger and Mourão 2008; Ribas et al. 2012; Leuchtenberger et al. 2015). Living in such suboptimal habitats and feeding on low quality and unusual prey, such as small benthic siluriform fish and snails (this study), as well as caimans (Ribas et al. 2012; this study) may have a direct effect on the health and survivorship of giant otters. Giant otters living in these lakes commonly have a debilitated appearance, with abnormal mucous membranes and dental defects (Ribas et al. 2012; Leuchtenberger et al. 2015; see Supplementary Data SD2). Living in these artificial lakes may impose a high fitness cost, because group size of otters monitored along the Estrada Parque Road usually decreased through time due to emigration and death of cubs (Leuchtenberger et al. 2015). Also, the long-term maintenance of groups depends on the seasonal connection of such lakes to a river system, allowing the renewal of fish stocks. Nevertheless, these groups could be an important source of individuals for translocation in reintroduction programs (Smith 2019).

Overlap between fisheries offtake and giant otter diets.—The overlap between otter diets and the catch of local fisheries was less than 40% for sport fishermen, and much lower (9.1%) for professional fishermen. The diet of giant otter groups included a larger set of prey species than the assemblages of fishes caught by fishermen. Prey of giant otters were mainly *Hoplias* and "piranhas" that also were the most frequent species consumed in other study sites (Duplaix 1980; Rosas et al. 1999; Cabral et al. 2010; Silva et al. 2014). However, the prey groups inhabiting rivers included other characiforms and siluriforms, which are important for professional fishermen. Although professional fishermen concentrate their effort on more valuable species, such as *Platystoma* catfish, sport fishermen catch a diverse assemblage, including the common "piranhas" and other fishes such as *Brycon*, *Leporinus*, and *Piaractus*. Otters search for fish during daylight under marginal vegetation, using vision and sensitive vibrissae to find their preferred prey, particularly *Hoplias* and *Serrasalmus*. These piscivorous and easy-to-catch fishes (Sazima and Machado 1990; Loureiro and Hahn 1996; Carvalho et al. 2002, 2007) inhabit lentic microhabitat at intermediate depths, near the river and lake margins under aquatic vegetation (Sazima and Machado 1990; Loureiro and Hahn 1996; Carvalho et al. 2002). During the flooding season, otter groups move long distances through flooded areas adjacent to the river channel, foraging for prey in the submerged vegetation. Professional fishermen also move longer distances at this time of the year, and adapt their fishing tools, locations, and strategies, according to the species of fish they aim to capture (Netto and Mateus 2009). Sport fishermen usually fish locations with easy access for motorboats, whereas professional fishermen choose the most productive fishing places, even when these are hard to access. Also, sport fishermen use fewer combinations of fishing strategies and tools than do professional fishermen (Netto and Mateus 2009). These differences allow professional fishermen to be more effective in selecting their prey.

According to the Fisheries Control System, from 2008 to 2011, a mean of 172 (*SD* = 46) professional fishermen and 718 (*SD* = 181) sport fishermen visited the study area ("Buraco das Piranhas") each year, resulting in an annual average of 21.5 t (*SD* = 3) and 9 t (*SD* = 2) of fishes caught by each category of fishermen, respectively (Albuquerque et al. 2011a, 2011b, 2012; Catella et al. 2017). However, these numbers represent a gross underestimate because it is known that many fishermen avoid the Environmental Police officers; as a result, numbers obtained from the Fisheries Control System are incomplete (A. C. Catella, pers. obs.). The estimated mean density of giant otters for the Buraco das Piranhas site was 0.42 ind/km^2 (*SD* = 0.004), which includes adults and juveniles (Leuchtenberger et al. 2015). Considering that the adult:juvenile ratio is about 70% (C. Leuchtenberger, pers. obs.) and that an adult giant otter eats approximately 3 kg (10% of their weight—Carter et al. 1999) of fish and other prey per day, the annual offtake by the Vermelho/Miranda otter population would be about of 37.8 t.

Although our study indicated that the diet of the otters did not overlap extensively with the assemblage of fishes taken by the fishermen, the giant otters do consume some of the fishermen's preferred species, such as large catfishes and *Piaractus*, and people often witness these occurrences. In addition, fishermen in the Pantanal believe that giant otters also affect local fisheries by interference when they pass through fishing areas (Zucco and Tomás 2004). Therefore, the perception that the species might overfish the fish stocks continues to be a trigger for human conflicts in areas of coexistence (Recharte et al. 2008, Rosas-Ribeiro et al. 2012; Lima et al. 2014), although the results presented here indicate that this perception largely is biased. Thus, educational programs are needed to inform the community and to reduce human conflicts with the species. The creation of guidelines to improve human–giant otter coexistence and social marketing are necessary to reduce conflicts between giant otters and fishermen.

Giant otters in the Pantanal primarily are piscivorous and their diet usually is concentrated on few species. Our study shows that this semiaquatic mammal has some degree of feeding plasticity when preferred prey are not available. Consumption of uncommon prey, such as small fish, snails, crabs, and even caimans, is evidence that giant otters can act as opportunistic predators when occupying suboptimal habitats. Considering the natural history of giant otters and their ecological restrictions, the interference of giant otters in fishing areas is inherent to the occurrence of the species in better fishing sites and in well-conserved locations. Although the piscivorous habit of the species is the main trigger for human conflicts, the overlap between the diet of otters and catches of sport and artisanal-professional fishermen is low and unlikely to impact these activities. Giant otters consume a varied prey base, which may reduce the overexploitation of fish stocks and allow the natural recruitment of prey species. Conservation initiatives, such as guidelines and social marketing to allow human–giant otter coexistence in fishing areas, are urgent to prevent increases in perceived human conflicts and to restore and safeguard relict populations. It is important to create programs to support the management of protected areas and indigenous grassroots organizations, as well as educational actions to inform fishermen and local people about the scant overlap between the otter's diet and fishing, and the importance of the species to maintain the balance of fish stocks; these actions must include guidelines as to how to deal with the presence of the giant otters at fishing sites. Some of the conflicts arise because local communities have few monetary sources and often look for a scapegoat to explain their problems. Creating economic alternatives, such as tourism, to secure the human coexistence with the species are essential for long-term conservation of giant otters.

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Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Linear regressions between the length of hard structures of fish and the standard length for nine fish species of the Southern Pantanal. Bands represent standard error (*SE*).

Supplementary Data SD2.—Teeth of two giant otters adult males captured for telemetry studies. Pictures A, B, and C show the teeth of an individual from a marginal lake that had several damaged teeth (see arrows on A). Picture D shows the teeth of an individual from a river. These animals were captured as part of a separate study (Leuchtenberger et al. 2013).

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