Raúl I. Vezzosi*, Ayelen T. Eberhardt, Vanina B. Raimondi, María F. Gutierrez and Andrés A. Pautasso

Seasonal variation in the diet of *Lontra longicaudis* in the Paraná River basin, Argentina

Abstract: We studied the Neotropical otter (*Lontra longicaudis*) seasonal diet variations in the middle Paraná River valley, in central-northern Argentina, at the southern limit of its global range. We recorded 745 prey items in 320 scats collected over the course of 1 year in a tributary stream of the Paraná River. Fish, crustaceans, mammals, and insects were the most important items in frequency of occurrence among items. Other items, like mollusks, birds, amphibians, and reptilians were presented in low frequency in all seasons. We recorded seasonal variation in the frequency of the principal categories items: fish, mammals, crustaceans, and insects and in reptilian that had low frequency. Although fish were the most common items consumed by the otter, other groups such as crustaceans, mammals, and insects, were also important in the diet of the Neotropical otter throughout the seasons. Mammals and insects showed a higher frequency in the Neotropical otter diet in our study than in Brazil, Mexico, and even northern Argentina. We noted a marked variation throughout the Neotropical region in the niche breadth indices among studies of Neotropical otter's diet. The Shannon *H'* diversity index showed a higher value in our study than in most of previous diet analyses of this species.

Keywords: feeding habits; Lutrinae; Mustelidae; Neotropical otter; Santa Fe.

***Corresponding author: Raúl I. Vezzosi,** Laboratorio de Paleontología de Vertebrados, Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción de Diamante, CONICET, Matteri y España s/n, (3105) Diamante, Entre Ríos, Argentina, e-mail: vezzosiraul@gmail.com
Ayelen T. Eberhardt: Laboratorio de Ecología de Enfermedades, Instituto de Ciencias Veterinarias del Litoral (UNL-CONICET), R. P. Kreder 2805, (3080) Esperanza, Santa Fe, Argentina
Vanina B. Raimondi: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" Av. Ángel Gallardo 470, (1405) Capital Federal, Argentina
María F. Gutierrez: Instituto Nacional de Limnología (CONICET-UNL), (3000) Ciudad Universitaria, Santa Fe, Argentina
Andrés A. Pautasso: Museo Provincial de Ciencias Naturales "Florentino Ameghino" Primera Junta 2859, (3000) Santa Fe, Argentina

Introduction

The Neotropical otter *Lontra longicaudis* is a semiaquatic carnivorous mustelid mammal in the all-American genus *Lontra* (Larivière and Jennings 2009). It is highly adaptable to a wide variety of tropical and temperate freshwater ecosystems including wetlands, riparian corridors, rivers, streams, lagoons, reservoirs, and artificial canals. It occurs from the north of Mexico to southeastern Argentina and Uruguay and from sea level to an altitude of 3885 m (Castro-Revelo and Zapata-Ríos 2001). It is the widest distributed otter of the three South American *Lontra* species (Gallo-Reynoso 1997, Larivière 1999, Barquez et al. 2006, Larivière and Jennings 2009). Although there are many records of the presence of the Neotropical otter at marine coasts (Blacher 1987, Schmidt et al. 2000, Alarcon and Simões-Lopes 2004), its feeding is concentrated in freshwater environments, even in coastal areas.

Some otter species are regarded as fish specialists in their feeding habits (Quadros and Monteiro-Filho 2001, Ottino and Giller 2004). However, several dietary studies indicate that Neotropical otter may be better defined as generalist carnivore (Gallo-Reynoso 1989, Wozencraft 1993, Spinola and Vaughan 1995, Macías-Sánchez and Aranda 1999). Its diet appears to be largely dependent on the availability of prey in the environment (Pardini 1998, Kasper et al. 2004a, 2008, Gallo-Reynoso et al. 2008, Bastazini et al. 2009, Perini et al. 2009). Such dietary flexibility seems to occur in other *Lontra* and *Lutra* species as well (Medina 1998, Ottino and Giller 2004, Preston et al. 2007, Medina-Vogel and Gonzalez-Lagos 2008).

The current knowledge of river otter feeding habits is based primarily on long-term studies of the Euroasiatic otter *Lutra lutra* (Foster and Turner 1991, Ottino and Giller 2004, Preston et al. 2007), the North American otter *Lontra canadensis* (Cote et al. 2008), and two South American species *Lontra felina* and *Lontra provocax* that were studied in southern temperate regions (Medina 1998, Medina-Vogel et al. 2004, Medina-Vogel and Gonzalez-Lagos 2008). The feeding habits of *Lontra longicaudis* has been studied in freshwater environments in Mexico (Gallo-Reynoso 1997, Macías-Sánchez and Aranda 1999, Casariego-Madorell et al. 2006, 2008, Gallo-Reynoso et al. 2008), Costa Rica (Macdonald and Mason 1992, Spinola and Vaughan 1995), Uruguay (Bardier 1992), and Brazil (Olimpio 1992, Helder and Andrade 1997, Pardini 1998, Colares and Waldemarin 2000, Quadros and Monteiro-Filho 2001, Kasper et al. 2004a,b, 2008, Quintela et al. 2008, Bastazini et al. 2009), as well as in the marine coastal area in southern Brazil (Alarcon and Simões-Lopes 2003, 2004).

In Argentina, at the southernmost extension of the distribution of Neotropical otter, only few dietary studies are available for this species (Parera 1992, 1993, 1994, Gori et al. 2003, Chemes et al. 2010). So far, no studies have been made about seasonal variations in its diet in the southernmost part of its range. Many aspects of its biology remain unknown, and its IUCN Red List status is "data deficient" (IUCN 2011). The conservation of Lutrinae is a priority in management of freshwater ecosystems due to the potential functional role that otters may have in freshwater ecosystems (Bifolchi and Lodé 2005).

Although there are several studies regarding the species diet (see above), there are, still, many aspects to be studied (e.g., seasonal diet in variations, feeding ecology, sprainting sites), especially when one compares the amount of knowledge gathered, so far, for other otter species. The present study aims to contribute to the knowledge about the seasonal feeding ecology of Neotropical otter by assessing the seasonal variations in the diet of *Lontra longicaudis* in a freshwater system from the alluvial plain of the Paraná River, the second largest South American river (Burkart et al. 1999). Additionally, we identified their primary prey in each season and examined any differences in their diet and compared the diet at this location in the southern portion of the range of the species with information from other regions. Such studies are needed not only because of potential interspecific differences between otter species but also due to distinct characteristics of the prey groups (e.g., fish species).

Materials and methods

Study area

The study was conducted in a riparian habitat alongside Arroyo Potrero, a stream located 35 km from the city of Santa Fe at 31°30′52″ S, 60°29′51″ W (Figure 1). This stream is part of the floodplain of the Leyes River that flows across the Paraná alluvial valley nearly perpendicular to the general direction of the Paraná River (Iriondo et al. 2007). Arroyo Potrero is characterized by a multiple use environment. There are boat jetties, boat ramps, and permanent weekend homes alternated with woody native vegetation of *Erythrina crista-galli*, *Salix humboldtiana*, *Acacia caven*, and *Tessaria integrifolia*. The downstream portion of the study area is a dense and continuous forest with *T. integrifolia* and *S. humboldtiana* as dominant trees (Figure 1). On sandy side hills is a dense forest with *S. humboldtiana* and *T. integrifolia* forming the upper and mid layers and with a dense understory of grasses and vines such as *Ipomoea alba*.

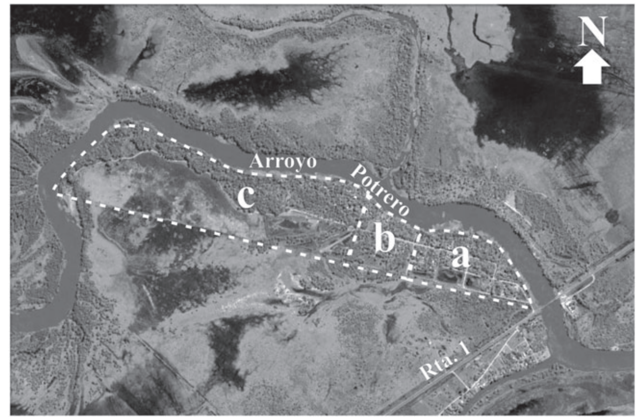

Figure 1 Map of the study area in the aluvial valley of Paraná River in Santa Fe, Argentina. (a) Area of boat ramps and permanent houses. (b) Transitional area with houses and native forest. (c) Study area with dense forest.

Scat collection and identification

In order to determine seasonal variation in otter diet, scats were collected weekly from September 2003 to September 2004. We collected scats from a 2-km stretch along Arroyo Potrero, from up to 10 m from the stream. We have only searched the left bank of the stream because the right bank was partly submerged, forming a wide flood plain.

In total, 320 scats were collected and analyzed. In cleaning the scat, we followed the methodology described by Kasper et al. (2008), with some modifications. Scats were bagged individually, labeled, sun dried, and stored in a bottle with laundry detergent for 24–30 h. After this period, feces were washed under running water in a fine meshed sieve (0.5 mm) to remove soluble material. The resulting items, composed of hard parts of ingested food, were air dried at room temperature for 24 h and stored in paper bags for later analysis.

With the aid of a stereoscopic microscope, we separated remains and structures that could potentially help to indentify the taxon of prey items. Mammals, birds, amphibians, reptiles, and fish remains were identified through their feathers, fur, teeth, scales, spiny rays, bone plates, vertebrae, and other anatomical structures. Insects and other invertebrates were identified by their hard parts. For identifications, we used the reference collection at the Museo Provincial de Ciencias Naturales "Florentino Ameghino" (Santa Fe, Argentina) and other reference works (i.e., Ringuelet et al. 1967, Brusca and Brusca 1990, Magalhães and Türkay 1996, Morrone and Lopretto 2001). Hard remains too damaged for clear identification were categorized as unidentified.

Statistical and quantitative analyses

In order to quantify the importance of each prey in the samples, the data were analyzed as the frequency of occurrence in scats (FO sensu Kasper et al. 2008) or the percentage of spraints that presented that item in relation to the total number of examined spraints (i.e., n=320)×100 (Jenkins et al. 1979) and the usually called "relative frequency" of a food item as percentage of occurrence (PO sensu Kasper et al. 2008). This last analysis shows the frequency of each food item divided by the sum of the frequency of all items (i.e., annual n=745)×100, the sum of the frequencies being 100% (Erlinge 1967, Perini et al. 2009). According to Kasper et al. (2008), the FO indicates how common an item is in the diet, while the PO indicates the importance of an item in the diet. Although the relative frequency of the items is often used in otter feeding ecology studies (e.g., Jacobsen and Hansen 1996, Pardini 1998, Gori et al. 2003, Kasper et al. 2004a, 2008, Medina-Vogel and Gonzalez-Lagos 2008), it may not accurately reflect the proportion of prey items actually consumed (Perini et al. 2009). This is because some prey items may yield no hard remains, and for prey with hard remains, there is uncertainty in inferring the number of individuals preyed on from multiple hard parts in a scat (Ottino and Giller 2004). However, the frequencies among item index are useful for inferring diet from scat, and it provides a standardized measure for seasonal and between-area comparisons (Perini et al. 2009).

We estimated dietary parameters by calculating sample richness (defined as the number of recorded taxa), Shannon diversity, and food-niche breadth to test seasonal variation in the otter diet. The data were grouped into periods of 3 months each (spring: October–December, summer: January–March, autumn: April–June, and winter: July–September). The undetermined items were included in all analysis. The change in dietary diversity was calculated using Shannon's H' index (Shannon and Weaver 1949) with 10 base logarithm. While the diet in seasonal changes was measured with Levins's B' index (Levins 1968, Krebs 1989). Finally, we compared the results obtained with those of other Neotropical otter studies (Parera 1992, 1993, Macías-Sánchez and Aranda 1999, Gori et al. 2003, Kasper et al. 2004a, 2008, Casariego-Madorell et al. 2008, Bastazini et al. 2009, Chemes et al. 2010).

To evaluate the seasonality in the diet composition, we used GLM with negative binomial responses (glm.nb function from the MASS package of the statistical software R) (Venables and Ripley 2002). For this analysis, we used the count of each item category (fish, mammals, crustaceans, insects, birds, reptilians, amphibians, and mollusks) in each scat. Undetermined items (e.g., unidentified cockroach, unidentified rodents) were also counted in each category. Likewise, the same analysis was used to evaluate the seasonality of fish and mammal families in the diet composition of Neotropical otter.

Results

Diet composition

We recorded 745 prey items in 320 scats collected at 12 sprainting sites along Arroyo Potrero. Fish was the most common prey of *Lontra longicaudis* in this area, present in 69% of the collected scats. Crustaceans (40%), mammals (24%), and insects (16%) were also frequent in the scats. All other prey categories appeared in the diet with low frequencies (<10%). At finer taxonomic resolution, the five most common prey categories were trichodactylid decapods (23%), callichthyid (15%) and prochilodontid fish (12%), and two terrestrial rodents: cricetids (17%) and caviids (11%).

Regarding diet items' frequency, for fish, we were able to quantify the occurrence of 349 individuals, representing 13 species and 11 families (Table 1). The three fish families with highest proportions among items were callichthyids (7%), prochilodontids (5%) and characids (5%), represented by two fish predators *Serrasalmus* sp. and *Salminus maxillosus*. Decapods trichodactylids were common among items (10%), with genera *Zilchiopsis* and *Dilocarcinus* most frequent (Table 1). Other invertebrates recorded were aquatic and terrestrial insects (belostomatids, beetles, orthopterans, and cockroaches) that were also frequent but occurred in low proportions (Table 1). Molluscs were present in a very low frequency (<1%). Amphibians and reptilians were represented by

Table 1 Seasonal percentage of occurrence (PO) and annual FO and PO among items, temporal variation of Levins *B′* niche breadth and Shannon *H′* diversity index of the prey consumed for diet of *Lontra longicaudis* in the Arroyo Potrero Stream, Santa Fe, Argentina.

Prey items	Spring (n=77)	Summer (n=52)	Autumn (n=69)	Winter (n=122)	Annual	
					FO	PO
Pisces	43.28 (103)	28.72 (27)	48.24 (82)	56.38 (137)	69.06	46.85
Prochilodontidae						
Prochilodus lineatus	3.78 (9)	4.26 (4)	8.24 (14)	4.94 (12)	12.19	5.23
Curimatidae						
Steindachnerina sp.			0.59 (1)		0.31	0.13
Leporinus obtudisens		3.19 (3)	0.59 (1)	1.23 (3)	2.19	0.94
Unidentified curimatids			0.59 (1)		0.31	0.13
Cichlidae						
Aequidens portalegrensis	2.94 (7)		1.76 (3)	2.47 (6)	5.00	2.15
Crenicichla sp.	0.84 (2)		2.35 (4)	2.06 (5)	3.44	1.48
Unidentified cichlids	0.42 (1)	2.13 (2)	0.59 (1)		1.25	0.54
Atherinidae						
Odontesthes bonariensis				1.23 (3)	0.94	0.40
Callichthyidae						
Unidentified callichthyids	11.34 (27)	1.06 (1)	2.94 (5)	7.00 (17)	15.63	6.71
Loricariidae						
Unidentified loricariids	2.94 (7)		8.82 (15)	1.65 (4)	8.13	3.49
Auchenipteridae						
Trachelyopterus sp.	5.04 (12)	1.06 (1)	2.35 (4)	2.88 (7)	7.50	3.22
Pimelodiae						
Pimelodus maculatus	2.52 (6)			1.23 (3)	2.81	1.21
Unidentified pimelodids	2.94 (7)		2.35 (4)	2.88 (7)	5.63	2.42
Characidae						
Serrasalmus sp.	1.68 (4)		1.76 (3)	8.64 (21)	8.75	3.76
Salminus maxillosus	0.84 (2)	1.06 (1)	0.59 (1)	0.82 (2)	1.88	0.81
Erythrinidae						
Hoplias malabaricus	0.84 (2)	1.06 (1)	0.59 (1)	1.23 (3)	2.19	0.94
Doradidae						
Pterodoras granulosus	2.10 (5)	1.06 (1)	2.94 (5)	0.82 (2)	4.06	1.74
Oxydoras kneri	0.42 (1)	2.13 (2)			0.94	0.40
Unidentified doradids	1.68 (4)		2.94 (5)	0.41 (1)	3.13	1.34
Unidentified fish	2.94 (7)	11.70 (11)	8.24 (14)	16.87 (41)	22.81	9.80
Crustacea	26.05 (62)	36.17 (34)	13.53 (23)	7.00 (17)	39.69	18.26
Trichodactylidae						
Zilchiopsis sp.	2.94 (7)	2.13 (2)	0.59 (1)		3.13	1.34
Zilchiopsis collastinensis	4.20 (10)	2.13 (2)			3.75	1.61
Zilchiopsis oronensis	0.42 (1)				0.31	0.13
Dilocarcinus sp.	6.30 (15)	6.38 (6)	1.76 (3)	1.65 (4)	8.75	3.76
Trichodactylus borellianus	0.84 (2)	2.13 (2)			1.25	0.54
Sylviocarcinus australis	0.42 (1)				0.31	0.13
Sylviocarcinus orenensis			0.59 (1)		0.31	0.13
Unidentified trichodactylids	10.92 (26)	23.40 (22)	10.59 (18)	4.12 (10)	23.75	10.20
Palaemonidae						
Palaemonetes argentinus				0.41 (1)	0.31	0.13
Macrobrachium borelli				0.82 (2)	0.63	0.27
Mollusca	5.04 (12)	2.13 (2)	2.94 (5)	2.47 (6)	7.50	3.36
Mitylidae						
Limnoperna fortunei	3.78 (9)	1.06 (1)	1.76 (3)	2.47 (6)	5.94	2.55
Ampullariidae						
Pomacaea sp. (eggs)	0.84 (2)	1.06 (1)			0.94	0.40
Unidentified gastropods	0.42 (1)		1.18 (2)		0.94	0.40
Oligochaeta						
Unidentified earthworms			0.59 (1)	0.41 (1)	0.63	0.27
Insecta	13.45 (32)	10.64 (10)	11.18 (19)	6.58 (16)	16.25	10.34

(**Table 1** Continued)

Prey items	Spring (n=77)	Summer (n=52)	Autumn (n=69)	Winter (n=122)	Annual	
					FO	PO
Odonata						
Libellulidae						
Unidentified libellulids		1.06 (1)			0.31	0.13
Orthoptera	1.68 (4)	1.06 (1)	0.59 (1)	0.41 (1)	2.19	0.94
Gryllidae						
Unidentified gryllids	0.42 (1)				0.31	0.13
Romaleidae						
Coryacris sp.		1.06 (1)	2.94 (5)		1.88	0.81
Hemiptera						
Belostomatidae						
Belostoma sp.	2.10 (5)	2.13 (2)	1.76 (3)	0.41 (1)	3.44	1.48
Coleoptera	2.10 (5)	1.06 (1)	0.59 (1)	1.23 (3)	3.13	1.34
Scarabaeidae						
Phileurus sp.				0.41 (1)	0.31	0.13
Dyscinetus sp.	0.42 (1)				0.31	0.13
Cyclocephala sp.	0.42 (1)				0.31	0.13
Unidentified scarabaeids	1.68 (4)			0.41 (1)	1.56	0.67
Dytiscidae						
Unidentified dytiscids		1.06 (1)		0.41 (1)	0.63	0.27
Staphylinidae						
Unidentified staphylinids				0.82 (2)	0.63	0.27
Noteridae						
Unidentified water beetles		1.06 (1)			0.31	0.13
Chrysomelidae						
Unidentified chrysomelids				0.41 (1)	0.31	0.13
Hydrophilidae						
Unidentified hydrophilids	1.26 (3)		0.59 (1)		1.25	0.54
Curculionoidae						
Unidentified curculionids	0.42 (1)		0.59 (1)	0.41 (1)	0.94	0.40
Blattodea						
Unidentified cockroach	1.26 (3)	2.13 (2)	1.18 (2)	0.41 (1)	2.50	1.07
Hymenoptera						
Vespidae						
Brachygastra sp.	0.84 (2)				0.63	0.27
Braconidae						
Unidentified braconids	0.42 (1)				0.31	0.13
Unidentified insects	0.42 (1)		2.94 (5)	1.23 (3)	2.81	1.21
Arachnida	1.26 (3)	1.06 (1)		0.41 (1)	1.25	0.67
Araneae	0.84 (2)	1.06 (1)			0.94	0.40
Opilionida	0.42 (1)			0.41 (1)	0.63	0.27
Amphibia	2.52 (6)	2.13 (2)	0.59 (1)	1.23 (3)	3.75	1.61
Anura	0.42 (1)		0.59 (1)	0.82 (2)	1.25	0.54
Bufonidae						
Rhinella sp.	0.42 (1)			0.41 (1)	0.63	0.27
Leptodactylidae						
Leptodactylus sp.	1.68 (4)	2.13 (2)			1.88	0.81
Reptilia	2.10 (5)	6.38 (6)	1.18 (2)	2.06 (5)	5.63	2.42
Ophidia	0.84(2)	2.13 (2)		1.23 (3)	2.19	0.94
Colubridae						
Hydrodynastes gigas	1.26 (3)				0.94	0.40
Helicops sp.		2.13 (2)		0.41 (1)	0.94	0.40
Philodrias patagoniensis				0.41 (1)	0.31	0.13
Unidentified colubrids		1.06 (1)			0.31	0.13
Viperidae						
Bothrops alternatus			1.18 (2)		0.63	0.27

(**Table 1** Continued)

Prey items	Spring (n=77)	Summer (n=52)	Autumn (n=69)	Winter (n=122)	Annual	
					FO	PO
Squamata						
Teiidae						
Teius sp.		1.06 (1)			0.31	0.13
Aves	1.26 (3)	3.19 (3)	1.18 (2)	4.12 (10)	5.31	2.42
Anatidae						
Anas versicolor				1.65 (4)	1.25	0.54
Accipitridae						
Rostrhamus sociabilis				0.41 (1)	0.31	0.13
Unidentified Scolopacidae		1.06 (1)			0.31	0.13
Furnariidae						
Agelaius cyanopus				0.41 (1)	0.31	0.13
Unidentified Furnariidae		1.06 (1)			0.31	0.13
Unidentified Passeriformes			0.59 (1)	0.82 (2)	0.94	0.40
Unidentified birds	1.26 (3)	1.06 (1)	0.59 (1)	0.82 (2)	2.19	0.94
Mammalia	3.36 (8)	8.51 (8)	19.41 (33)	18.52 (45)	23.75	12.62
Cricetidae						
Holochilus sp.	0.84 (2)	3.19 (3)	8.24 (14)	9.47 (23)	13.13	5.64
Oligoryzomys flavescens		2.13 (2)	1.76 (3)	3.70 (9)	4.38	1.88
Caviidae						
Cavia aperea	1.68 (4)	3.19 (3)	8.82 (15)	4.94 (12)	10.63	4.56
Unidentified rodents	0.84 (2)		0.59 (1)	0.41 (1)	1.25	0.54
Unidentified taxa	1.68 (4)	1.06 (1)	1.18 (2)	0.82 (2)	2.81	1.21
Shannon H′	0.64	0.28	0.47	0.62	0.71	
Levins B′	0.3	0.4	0.3	0.2	0.27	

n, number of scats analyzed per season; Parentheses, number of individual prey; Seasonal PO was calculated separately (item frequency sum for each season=100).

remains of semiaquatic species, and colubrid and viperid snakes occurred in the diet in low proportions (<1%). Bird remains occurred as feathers, fragmented bones, and one beak and were ascribed to silver teal (*Anas versicolor*, Anatidae), sandpipers (Scolopacidae), snail kite (*Rostrhamus sociabilis*, Accipitridae), and unicolored blackbird (*Agelaius cyanopus*, Icteridae).

For the year-round totals, both Shannon-Weaver and Levins indices had high scores, indicating a varied diet composition (Table 1). Our comparison between regions of the standardized niche breadth indices showed marked variations throughout the Neotropical region and similarities between Brazilian and Argentinian environments (Table 2).

Seasonal variation in the diet composition

Proportions of prey taxa showed variations in all seasons (Table 1). The PO of fish was the most important item category throughout the seasons except in summer where the crustaceans had the higher occurrences (Figure 2). Crustaceans had the second higher occurrence in spring. However, consumption of mammals presented higher values than crustaceans in both autumn and winter seasons. Insects were most frequent in the diet in spring (Figure 2).

Among invertebrates preyed group, the presence of aquatic paleomonids crustaceans were recorded only three times in winter scats, while decapod trichodactylids had variations in the diet with *Dilocarcinus* sp. prey as the highest occurrence during the spring-summer period (Table 1). Other items, like molluscs, birds, amphibians, and reptilians were presented in low frequency in all seasons (<5%, Table 1).

The mussel *Limnoperma fortunai* had the highest occurrences in winter-spring period (Table 1), being recorded in the same scats that occur doradids and curimatids fish. Also, gastropod eggs of *Pomacaea* sp. are recorded during spring-summer and carapace only on spring and autumn. Aquatic and terrestrial insects are well recorded over winter, spring, and summer with beetles, and in autumn with orthopterans. The aquatic *Belostoma* sp. and cockroach had low values on all seasons.

Table 2 Shannon's *H′* diversity and Levin's *B′* niche breadth comparison between diet analyses of Neotropical otter *Lontra longicaudis* in South America, considering all the prey categories found in the otters scats.

Diversity index H′		Locality
0.71		Arroyo Potrero, Santa Fe (31°30′52″ S–60°29′51″ W)
0.58		Parque Nacional El Rey, Salta (Chemes et al. 2010)
0.09		Río Iguazú, Misiones (Parera 1993)
0.26		Laguna Iberá, Corrientes (Parera 1992)
0.60		Laguna Iberá, Corrientes (Gori et al. 2003)
0.72	(dry season)	Río Los Pescados, Veracruz (Macías-Sánchez and Aranda 1999)
0.46	(wet season)	Río Los Pescados, Veracruz (Macias-Sánchez and Aranda 1999)
1.00		Río Zimatán, Oaxaca (Casariego et al. 2008)
0.95		Río Copalita, Oaxaca (Casariego et al. 2008)
0.69		Río, Ayuta, Oaxaca (Casariego et al. 2008)
Levins index B′		Locality
0.27		Arroyo Potrero, Santa Fe (31°30′52″ S–60°29′51″ W)
0.24		Taquari Valley (Kasper et al. 2004a)
0.20		Taquari Valley (Kasper et al. 2008)
0.21		Brazil (Bastazini et al. 2009)

Only one taxon bird (*Anas versicolor*) had the highest frequency in winter with four presences in the scats. The amphibians and colubrids had no records in autumn scats than viperid prey *Bothrops alternatus*. The semiaquatic colubrids preyed, *Hydrodynastes gigas* and *Helicops* sp., have shown the highest occurrence on spring and summer seasons in the diet, and the tegu lizard (*Teius* sp.) only had reported on winter with low frequency of occurrence (Table 1).

Items category differences between seasons

Fish consumption was significantly higher in winter than in spring and autumn (p=0.008 and p=0.011, respectively), whereas the crustaceans was greater and significant in autumn (p<0.001), winter (p=0.003), and summer (p<0.001) vs. spring. Most of the mammal preys were consumed in winter and spring seasons than in autumn (p=0.013 and p<0.001, respectively). Considering the

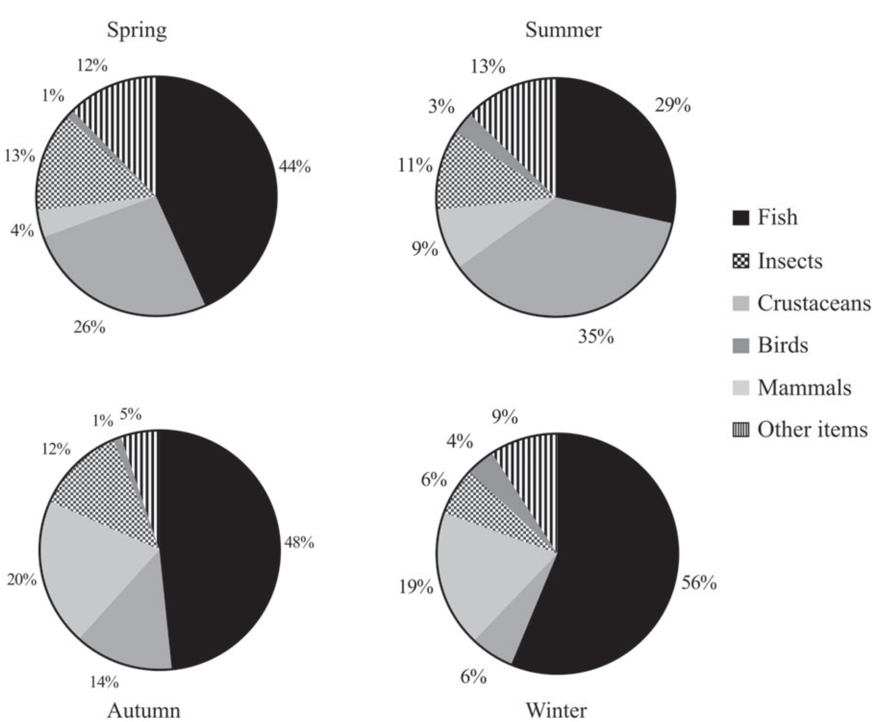

Figure 2 Seasonal changes in the Neotropical otter diet. Relative percentage of ocurrence (PO) of major food items between seasons. Frequencies were calculated separately (items frequencies sum for each season=100).

insects, only significant difference was observed between spring and autumn; in the latter, the consumption was highest (p=0.048). The only difference in the reptilian categories was between autumn and winter, and in the first one, the ocurrence was higher (p=0.04).

Among the fish families, in autumn, the curimatids showed a strong occurrence and was significantly highest than in winter and in spring (p=0.031 and p=0.049, respectively). In the spring, the callichthyids were greater than in the other seasons (vs. autumn, p=0.001; vs. winter, p=0.003; vs. summer, p=0.004). Moreover, the caracids had a higher occurrence in cold-temperature periods than in the middle (autumn, p=0.031) and warm seasons (summer, p=0.023). In cool seasons, the loricariids were more frequent in autumn than in winter (p<0.001), while the Doradidae (omnivorous doradids) showed an increase during autumn (p=0.007) and spring (p=0.011) than in winter. Likewise, in the spring, the occurrence of auchenipterids fish were significantly higher than in winter (p=0.035) and summer (p=0.04). However, other fish families had no significant differences between seasons in the Neotropical otter diet, though it is interesting to note that the migrant *Odontesthes bonariensis* was only present in the diet in winter with low occurrence (Table 1).

Furthermore, in the mammal's prey, the Cricetidae family was more frequent significantly in winter than in spring (p=0.001) and summer (p=0.037) and had more occurrence in autumn than in spring (p=0.003). Likewise, the Caviidae rodents showed the highest frequency of occurrence in autumn than in other seasons (vs. winter, p=0.041; vs. primavera, p=0.011; vs. summer, p=0.036).

Discussion

Neotropical otter's diet

Many studies have shown the piscivorous character of the Neotropical otter diet, with consumption of other prey groups, other than fish, varying throughout its area of distribution (Parera 1992, 1993, Pardini 1998, Macías-Sánchez and Aranda 1999, Colares and Waldemarin 2000, Quadros and Monteiro-Filho 2001, Gori et al. 2003, Kasper et al. 2004a, 2008, Chemes et al. 2010). In our study, although fish were the most common items consumed by the otter, other groups, such as crustaceans, mammals and insects, were also important in the diet of the Neotropical otter throughout the seasons and show major proportions than those recorded in freshwater environments in Brazil, Costa Rica, Mexico, and even in northern Argentina.

We found mammal items to be a frequent component in the diet, whereas this prey was recorded with a low proportion, or even absent, in previous studies of the *Lontra longicaudis* (Pardini 1998, Gori et al. 2003, Kasper et al. 2004a, 2008, Quintela et al. 2008, Chemes et al. 2010). The low occurrence of terrestrial vertebrate prey in the diet of different populations studied in Argentina (Parera 1992, 1993, Gori et al. 2003, Chemes et al. 2010) could be explained by methodological biases (e.g., low number of scats sampled) or absence of year-round sampling. Although, mammals such as rodents are common in the diets of some terrestrial predators in the Paraná River basin riparian environments (Pautasso 2006, 2008, Canesini et al. 2008), in the diet of Neotropical otter, the presences of rodents prey have been considered occasional or even rare (Kasper et al. 2008, Quintela et al. 2008, Chemes et al. 2010). Here, we verified and have found that these terrestrial animals would be an important category in the diet of the Neotropical otters with higher and shirting values in the seasons and a high taxonomic rodents richness prey more than in Brazil and Mexico.

In turn, the highest occurrences of terrestrial prey recorded in scats of both winter and spring could be related to an energy need by the emergence of cubs (Green et al. 1984, Mason and Macdonald 1986) or to the reinforcement of dominance relationships within the otter population when young animals become independent and establish their own home ranges (Ottino and Giller 2004). Over the spring-summer seasonal period, we found that the sprainting sites were used by a female with two cubs.

Preys such as amphibians and reptilians have showed low proportions as in other South American diet studies (Colares and Waldemarin 2000).

Earthworms have been rarely mentioned in otter diet and have shown low occurrence in the scats (Southern 1964, Fairley 1972, Chanin 1981, Ottino and Giller 2004). Here, this low proportion in the diet (>1%) may be considered an occasional consequence of food item, taken by the *Lontra longicaudis* directly near the scat sites (Ottino and Giller 2004), or even also, as a secondary prey like *Limnoperna fortunai*. This type of invertrebrate is commonly considered as a marked food item in the fish diets of the Paraná basin (Oliveira et al. 2010, Esper Amaro de Faria and Benedito 2011) and also has a positive effect on fish biomass (Ferriz et al. 2000, Cantanhêde et al. 2008).

Wetland birds that we found as *Lontra longicaudis* prey are associated with freshwater environments. For instance, the snail kite (*Rostrhamus sociabilis*) is abundant in freshwater environment of the Neotropical otters, where it preys on aquatic invertebrates, primarily snails (Magalhães 1990, Veiga et al. 2009). Thus, some birds that were consumed would be vulnerable to stalking attack by *Lontra longicaudis* in riparian vegetation as reported by Macías-Sánchez and Aranda (1999) and Gallo-Reynoso et al. (2008), due to some birds that consume many types of aquatic prey like invertebrates or fish (Magalhães 1990, Rozzatti et al. 1995, Latino and Beltzer 1999, Veiga et al. 2009). According to Schoener (1971), the feeding strategy of the *Lontra longicaudis* is considered a response that presents many medium and large carnivores, for which the selection of prey would depend more on the facility with which it could be taken than on their relative abundance in the environment, which may indicate that aquatic birds are more vulnerable prey available for the Neotropical otters.

Seasonal prey's fluctuations

For fish, we found seasonal variations in the families captured by the *Lontra longicuadis*, a similar result as in the previous studies from other Neotropical regions (Passamani and Camargo 1995, Helder and Andrade 1997, Pardini 1998, Colares and Waldemarin 2000, Quadros and Monteiro-Filho 2001, Gori et al. 2003, Kasper et al. 2008, Chemes et al. 2010). Seasonal variation in the fish families captured is probably related to availability and seasonal changes in the environment where these families live (Kasper et al. 2008, Quintela et al. 2008). The cichlids and loricariids have been pointed out as the most frequently consumed prey of *L. longicuadis* in Neotropical environments (Helder and Andrade 1997, Pardini 1998, Gori et al. 2003, Kasper et al. 2004a,b, 2008; Quintela et al. 2008, Chemes et al. 2010), but we found these families at low proportions, even when compared to nearby regions in Brazil and northeastern Argentina (i.e., the Iberá wetlands in Corrientes) (Gori et al. 2003).

Comparing our results with those of Gori et al. (2003) and Kasper et al. (2008), it is possible to verify a feeding pattern for *Lontra longicaudis* between seasons in this region, where fish is a major component of its diet, but there is a high occurrence in the consumption of other groups of prey as mammals and semiaquatic invertebrate.

The freshwater communities in streams and rivers of the Paraná basin are strongly influenced and stimulated by environmental conditions (Collins and Paggi 1998, Armúa de Reyes and Estévez 2005, Armúa de Reyes and Kehr 2005, Collins et al. 2004, 2009), such as seasonal changes and alterations in the hydrometric level of the basin (Bonetto 1986, Collins and Paggi 1998, Bó and Malvárez 1999, Baigún and Oldani 2006). These natural conditions may also reflect temporal fluctuations in availability and relative abundance of certain prey items for otters (Ottino and Giller 2004, Kasper et al. 2008), which are involved by fluctuations of the water level of the Arroyo Potrero stream (Appendix 1 – online supporting data) depending on the seasonal hydrodynamic of the larger Paraná River system (Bonetto 1986, Iriondo et al. 2007).

According to Pardini (1998), the predation by *Lontra longicuadis* on certain aquatic items seems to be selective, and the occurrence in scats usually is not proportional to their relative abundance in South American rivers and streams from Brazil. This hypothesis is not corroborated here because we did not measure prey availability and abundance in the habitat where our study was concentrated. Nevertheless, we found that *L. longicaudis* does not feed on different items with the same frequency in all seasons. That could be interpreted as a result of changes in prey availability. Otters are usually regarded as opportunist predators, as they inhabit many types of aquatic environments and are capable of exploiting different kinds of prey in each of them (Pardini 1998, Ottino and Giller 2004, Kasper et al. 2008). This would be the main reason why seasonal changes in the contribution of prey items to *L. longicaudis* diet have often been interpreted as a result of changes in prey availability, even when this variable was not measured (Olimpio 1992, Spinola and Vaughan 1995). However, the few studies that have analyzed prey availability show that otters choose particular kinds of prey or even classes of prey size (Van der Zee 1981, Wise et al. 1981, Kruuk and Moorhouse 1990), as tegu lizards, armadillos, Neotropic cormorant, even potential competitors as opossums or skunks (Rossi-Santos 2007, Gallo-Reynoso et al. 2008, Quintela et al. 2008, Quintela and Gatti 2009), as well as some fish, snail kite, and snakes that were found in this study. All these species come in various sizes, from small to midsized, depending on their age. These preys may be hunted by stalking behavior underwater or through riparian vegetation, but could also be carrion or have been injured before predation by the Neotropical otter (Gallo-Reynoso et al. 2008, Quintela and Gatti 2009, Muanis and Oliveira 2011). Several species of midsized and large mammal species (i.e., *Conepatus chinga*, *Hydrochaeris hydrochaeris*, *Procyon cancrivorus*, *Cerdocyon thous*) live with the *L. longicaudis* in the Paraná River's riparian environments (Canesini et al. 2008, Pautasso 2008), but were not found in the scats we have collected.

Thus, it is probable that environmental fluctuations, prey availability, prey microhabitat, conspicuousness, and palatability could be some factors that influences the prey selection and not only differences in dentition in the otters species or escape ability and size of prey (Pardini 1998, Kasper et al. 2004b, Perini et al. 2009).

Diversity indices

There is a lack of information about the basic ecology of Lutrinae referred to in the niche breadth analyses in which there are difficulties in comparisons between freshwater environments. Macdonald (2002), in a revision about mustelids in Great Britain, finds for *Lutra lutra* a mean value of its niche breadth sensibly inferior to the preliminary results for the *Lontra longicaudis* in Brazil (Bastazini et al. 2009). The few preliminary conclusions about this analysis in *L. longicaudis* have shown a fish specialist feeding habit (Macías-Sánchez and Aranda 1999, Kasper et al. 2008, Bastazini et al. 2009). In Brazilian environments, the standardized form of Levins' index used in the diet of *L. longicaudis* (Kasper et al. 2008, Bastazini et al. 2009) have proved similar values of niche breadth to the mean value recorded in this study. But the presence of some terrestrial prey in the scats was the most significant prey, in terms of proportions, that show a more generalist feeding habit to the *L. longicaudis* for this austral area of de Paraná valley, due to the environmental heterogeneity observed in the Arroyo Potrero stream.

Bastazini et al. (2009), report a significantly positive correlation between the niche breadth and latitude in Brazil, and therefore, they conclude that the Gause's hypothesis could be expanded to populations of species that are distributed along a latitudinal gradient, such as the Neotropical otter *Lontra longicaudis*. Information on the geographical variation of niche breadth of other species that are distributed along a latitudinal gradient, like the one present in the austral region of Paraná basin, would be of great importance to elucidate this question.

We found a higher Shannon's diversity index (H'=0.71) than in previous *Lontra longicaudis* diet analyses from Argentinian environments and very similar to the results from the northern regions. Chemes et al. (2010) presented a Levin's index that actually was a Shannon-Weaver's index and incorrectly compared this index with other diet studies from Argentina. We recalculated their Shannon-Weaver's index and found a higher value (H'=0.58) than in previous otter diet studies from Argentina, but less than our results.

Shannon index values for *Lontra longicaudis* diet relate to the piscivorous character of the species (Kasper et al. 2008), with consumption of other important group of non-fish prey varying throughout its area of distribution, including crustaceans (Pardini 1998, Colares and Waldemarin 2000), reptiles (Rossi-Santos 2007), mammals (Quintela et al. 2008, Quintela and Gatti 2009), birds (Gallo-Reynoso et al. 2008), insects (Gori et al. 2003), fruits and vegetables (Quadros and Monteiro-Filho 2000). Most of these food categories, except fruits and vegetables, recorded in this study had a more proportions even in different seasons than other Neotropical regions.

In summary, we found a varied diet of the Neotropical otter in a tributary stream of the Paraná River, with marked seasonal variation that probably reflects availability variation in prey related to fluctuations in water levels. The breadth of its food spectrum and its position as top predator indicate a potential importance in maintaining ecosystem functioning in its aquatic environment.

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