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Diet composition of an invasive population of Lithobates catesbeianus (American Bullfrog) from Argentina

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The American bullfrog *Lithobates catesbeianus* has been introduced around the world, with invasive populations reported from almost all South American countries. A population of this species was introduced in the Calingasta department of San Juan province, which is an arid environment in western Argentina. This work provides information on the dietary composition of an invasive population of *L. catesbeianus*, and compares the degree of dietary overlap between adults and juveniles. Stomach contents of 169 bullfrogs (82 adults and 87 juveniles) were analysed. Adults consumed 40 prey taxa and Hymenoptera (Insecta) was the most numerous prey item (41.8%), followed by Araneae (13.6%) and Aeglidae (13.4%). Juveniles consumed 29 prey taxa and Hymenoptera constituted the highest percentage in prey number (77.2%). The trophic overlap niche index at the same level shows a value of 0.64 overlap in dietary community between adults and juveniles of this bullfrog. Aeglidae was volumetrically the most important trophic item (25.4%), followed by Anura (25.02%). Our results showed that cannibalism in bullfrogs is more common than the consumption of native anurans, coinciding with that reported in other populations of introduced bullfrogs. The high similarity in the diets of both size classes and the association between the size of the predator and prey suggest that the impact caused by bullfrogs throughout their ontogeny is high and probably has an impact on their prey. Freshwater crabs are the main items in the diet of *Lithobates catesbeianus* in other introduced populations and are usually the most conspicuous at our study site. The crabs in freshwater ecosystems are part of the lowest trophic level in the food chain. The major threats to the southern region's freshwater crabs include deforestation, farming and exotic species. *Lithobates catesbeianus* has a generalist diet and high overlap between adults and juveniles.

Keywords: American bullfrog; Amphibian; Argentina; invasive population; *Lithobates*

Introduction

Introduction of non-native species by humans is a growing biological and economic concern. The American bullfrog, *Lithobates catesbeianus*, is considered one of the world's worst invaders (Lowe et al. 2010). This bullfrog has been introduced around the world in Austria, Belgium, Brazil, Canada, Chile, Canary Islands, China, France,

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Ecuador, Germany, Mexico, in different places in the United States of America, Venezuela, Great Britain, Cuba, Colombia, Greece and Argentina (Kraus 2009). It has been suggested that *L. catesbeianus* affects native frog species through direct predation and interference competition (Werner et al. 1995; Kiesecker and Blaustein 1998; Pearl et al. 2004). Impacts include biotic homogenisation, disruption of food webs, changes in primary productivity, changes in soil formation, and parasite and disease introduction, which can contribute to the extinction or extirpation of native species (Kraus 2009; CABI 2013). The bullfrog is an asymptomatic vector of the emerging fungal pathogen *Batrachochytrium dendrobatidis* (*Bd*) of amphibians (Daszak et al. 2004). However, recent studies have shown that bullfrogs may be susceptible to certain known strains of *Bd*, and resistant to others. Perhaps bullfrogs are an inefficient carrier or a reservoir of *Bd* (Gervasi et al. 2013). *Bd* has caused the decline of many amphibian populations worldwide (Bosch et al. 2001; Schloegel et al. 2010), and the consequences of introduced vectors can be destructive to native species and the environment (Begon et al. 2006).

Lithobates catesbeianus has a generalised diet (Werner et al. 1995; Hirai 2004; Boelter and Cechin 2007; Texeira Da Silva et al. 2009) consisting primarily of insects and crustaceans, often overlapping with the diet of native frogs (Kupferberg 1997; Kiesecker and Blaustein 1998; Lawler et al. 1999; Kiesecker et al. 2001; Boone et al. 2004). Also, bullfrogs consume small vertebrates such as fish (Korschgen and Moyle 1955; Corse and Metter 1980), frogs (Mckamie and Heidt 1974; Hays 1985; Sanabria and Quiroga 2010), turtles (Corse and Metter 1980; Graham 1984), snakes (Minton 1949), birds (Gollop 1978), bats (Lee 1969) and weasels (Beringer and Johnson 1995).

The native range of the American bullfrog extends from eastern Canada through the central and eastern United States, to northeastern Mexico. This species has been widely introduced around the world and invasive populations have been reported in almost all countries in South America (Frost 2013). Populations of *L. catesbeianus* have been reported from Argentina in the provinces of San Juan (Sanabria et al. 2005; Sanabria, Ripoll, et al. 2011), Misiones (Pereyra et al. 2006), Buenos Aires (Barrasso et al. 2009), Córdoba (Akmentins et al. 2009; Nori et al. 2011), Salta (Akmentins and Cardozo 2010) and Mendoza (Sanabria, Debandi, et al. 2011). In Argentina, information about the impacts of *L. catesbeianus* on native species is limited; the only study from Buenos Aires on introduced bullfrogs analysed the diet composition of captured frogs (Barrasso et al. 2009). Most studies that have evaluated the impact of farmed populations of bullfrogs in different ecosystems have been concentrated in North America, Europe and parts of Asia, but have scarcely studied in South American ecosystems. This is the first study to analyse the composition of the diet of an introduced population of *L. catesbeianus* in an arid environment of mid-elevation in the central Andes of Argentina. Our aim is to analyse the dietary composition of an invasive population of *L. catesbeianus* and to evaluate the degree of dietary overlap between adults and juveniles. This work provides basic information that can help identify impacts of this species and help with future management decisions.

Materials and methods

The study area is located 130 km west of the city of San Juan, in the Calingasta department of San Juan province, Argentina (31.2515°S, 69.4417°W; elevation 1331 m; Figure 1). The bullfrog population was introduced accidentally in the 1980s. A truck carrying a container with bullfrog tadpoles for a commercial breeding farm overturned when crossing the Castaño Viejo River (Sanabria et al. 2005). This site has

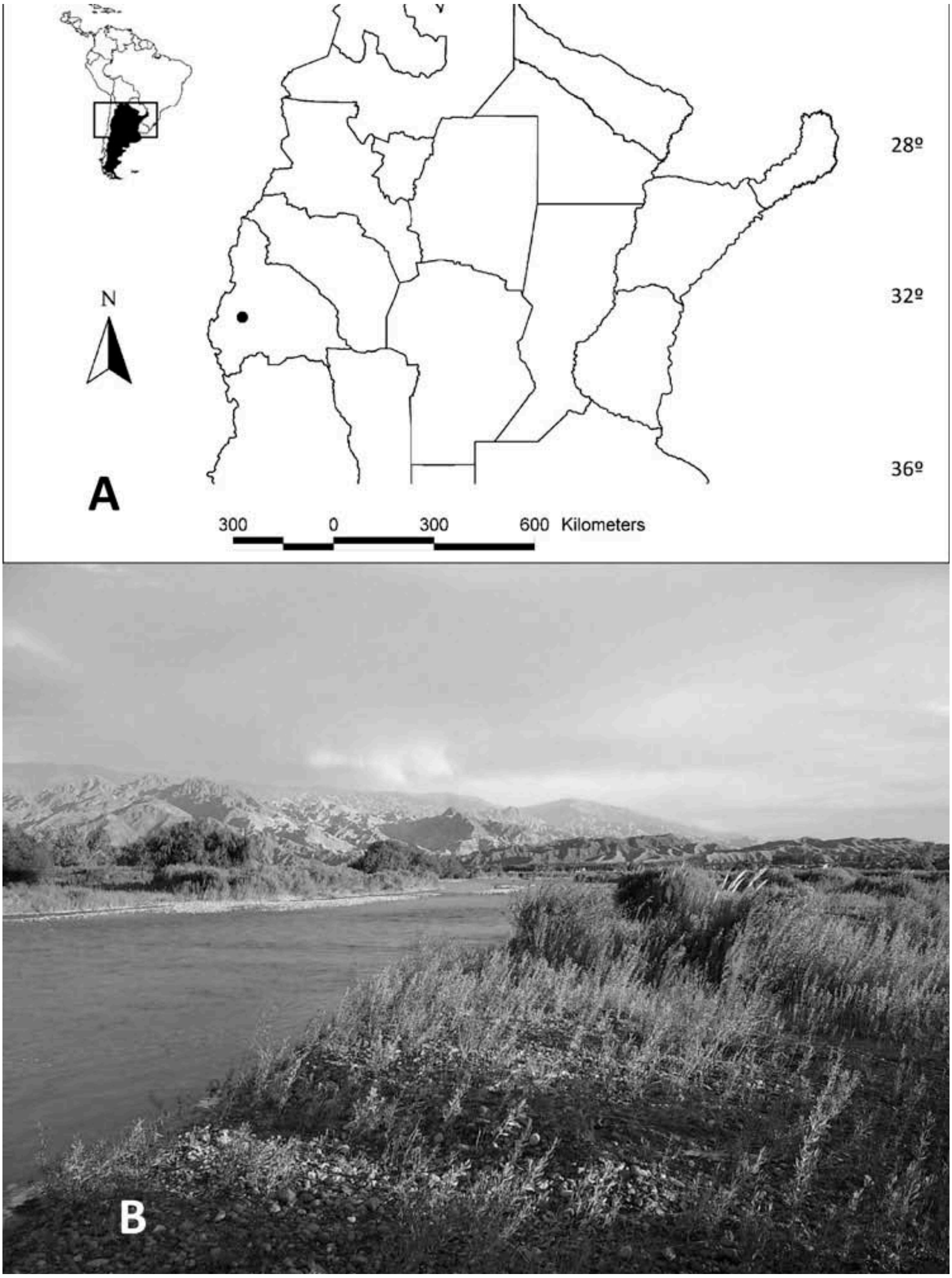

Figure 1. (A) Location of studied invasive population of *Lithobates catesbeianus* from San Juan (black dot); (B) typical environment where the bullfrogs were captured for this study, around the Castaño Viejo River.

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been determined to be the origin of the bullfrog invasion in San Juan. The region belongs to the Monte de Sierras and Bolzones ecoregions (Pol et al. 2006). The area has an arid climate with a mean annual temperature of 17.3°C, a maximum mean annual temperature of 25.7°C, a minimum mean annual temperature of 10.4°C, and a mean annual rainfall of 89 mm concentrated mainly in summer (Cabrera 1994). The dominant vegetation includes *Cortaderia* sp., *Typha dominguensis, Tessaria absinthioides, Prosopis strombulifera*, *Prosopis* sp., *Atriplex* sp., *Larrea* spp. and *Bulnesia retama*, among others.

We used different colouration patterns to determine size classes. Adults have a distinct dorsal colouration (olive, green or brown above, often light green on their head; legs banded and blotched dusky with some spotting on back) and show sexual dimorphism and nocturnal activity; juveniles typically have a bright green dorsal pattern, diurnal/crepuscular activity and alarm calls (Stebbins 2003). In our study population, the largest individual showing the colouration pattern of juveniles was 59 mm snout-vent length (SVL), which we considered as the body size limit for separating adults (SVL > 60 mm) and juveniles (SVL ≤ 59 mm). The colouration pattern is a good indicator of the sexual age, and the sexual dimorphism (accompanied by sexual maturation) allowed us to separate sexes, and adults from juveniles.

We visited the study area for 3 days on each field trip, and a total of 169 bullfrogs were captured by hand (Table 1). We examined the study area by nocturnal/diurnal hazard walks along the river with a team of six people over 8 h (from 1800 to 2100 h and 2200 to 0200 h), using the visual encounter survey technique (Heyer et al. 2001). We searched all microenvironments available in the study area (4.92 km^2), including river edges, grasslands and both temporary and permanent pools (Figure 1). Specimens were immediately euthanised by injection of 2.5 mL of anesthesia [2% Xylocaine, 2% lidocaine hydrochloric acid (HCl), AstraZeneca Lab] into the frog's lymph sac, then fixed in 10% formalin and preserved in 70% alcohol. Body length (SVL) was measured with a digital calliper (Essex, China 0.01-mm precision).

The stomach was separated from the intestine between the cardiac and pyloric sphincters for dietary analysis, and the contents viewed under a binocular stereoscopic magnifying glass (2–40× magnification; Arcano, China). The length and width of each individual prey item was measured with a digital caliper, and prey volume was obtained by applying the elliptical sphere equation (Dunham 1983):

$$v = {}^{4}/_{3}\,\pi\left({}^{L}/_{2}\right)\left({}^{W}/_{2}\right)^{2} \tag{1}$$

Table 1. Date and number of juveniles and adults of *Lithobates catesbeianus* captured for this study.

Date	N juvenile	N adult
November 2004	–	12
December 2009	33	2
January 2010	–	26
October 2011	21	29
February 2012	33	13
Total	87	82

where L is the length and W is the width of each prey item.

Prey items were classified to the lowest taxonomic level allowed by their state of decomposition, based on reference guides by Bland and Jaques (1978) and Brewer and Arguello (1980). Prey items conserving key identification structures (heads, forewings) were considered individuals.

Descriptive statistics (mean ± standard error) were used to characterise the morphometric variables of predator and prey. The trophic niche breadth of each size class was defined using Levins' index (Levins 1968):

$$Nb = 1/\sum_{i=1}^{n} Pi_{\ 2} \tag{2}$$

where i is the prey category, p is the proportion of individuals associated with the prey category i and n is the total number of prey categories represented in the diet. Trophic niche breadth values range from 1 (utilisation of only one prey type) to n (all prey types used equally). An index of relative importance (IRI) was used to compare the dietary contribution of each food category (Pinkas et al. 1971):

$$IRI = \%FO(\%N + \%V) \tag{3}$$

where %FO is the frequency of occurrence of a food category, and %N is the numerical percentage, and %V the volumetric percentage, of the prey items. Jaccard's similarity index, which measures similarity between qualitative variables at the family level, was used to determine the dietary similarity between adults and juveniles (Moreno 2001). The dietary overlap between size classes was calculated using the index of Pianka (1973). Diet overlap between predator groups j and k was calculated as:

$$Ojk = Okj = \frac{\sum(Pij\,x\,Pik)}{(\sum Pij^2\,x\sum Pik^2)^{0.5}} \tag{4}$$

where pij and pik are the relative abundance of prey category used by group j and k paired in each treatment. $O_{jk} = O_{kj}$ means that the effect of group j on group k is equal to the effect of group k on group j.

Also, for the relationship between size of predator (SVL) and mean length prey (MLP) in bullfrog stomachs, we used the Pearson's regression test. We used the PAST version 9.4 (Hammer et al. 2001) statistical packet for statistical analyses (Pearson's regression test and descriptive statistics).

Results

Of the 169 bullfrogs collected, 82 were classified as adults and 87 as juveniles. The gastrointestinal contents of adults included 506 prey items, which were assigned to 40 taxa. For juveniles, we identified 974 prey items assigned to 29 taxa (Table 2). The trophic niche breadth value for adult frogs was N_b = 5.38, and for juveniles it was N_b = 3.45.

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Table 2. Dietary composition of invasive population of *Lithobates catesbeianus* by size class (N_{Adults} = 82, $N_{Juvenile}$ = 87).

Prey category	Adults		Juvenile	
	N	IRI	N	IRI
CHORDATA				
Anura				
Ranidae	3	8.83	1	2.90
Lithobates catesbeianus				
Ni (no Ranidae)	4	8.69		
Cyprinodontiformes				
Poecillidae				
Jenynsia multidentata	1	0.18	2	0.69
Characiformes				
Characidae			1	2.90
Mollusca				
Planorbidae	5	0.51		
Lymnaeidae	27	33.47	23	6.59
Planorbidae			1	0.5
Ni			2	0.12
ARTHROPODA				
Decapoda				
Anomura				
Aeglidae	68	811.6	24	412.27
Insecta				
Coleoptera				
Cicindelidae	1	0.08		
Scolytidae			1	0.06
Dystiscidae			6	1.72
Tenebrionidae	7	0.63		
Elateridae	3	0.26	1	0.06
Carabidae	4	1.12	8	2.48
Coccinelidae	7	2.59		
Curculionidae	12	9.82	7	4.68
Larva	8	0.73		
Ni	13	8.08	17	14.35
Diptera				
Stratiomyiidae	1	0.08		
Calliphoridae	1	0.09		
Drosophilidae			2	0.13
Larva	5	4.89	6	1.22
Tabanidae	5	0.88	24	11.56
Muscidae	1	0.09	3	0.41
Tipulidae	2	0.17		
Culicidae	2	0.35		
Ni	2	0.35	3	0.61
Hemiptera				
Belostomatidae	2	0.59	11	8.43
Coreidae	1	0.50	1	0.20

(*Continued*)

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Table 2. (Continued).

Prey category	Adults		Juvenile	
	N	IRI	N	IRI
Ni	2	0.17	6	1.62
Hymenoptera				
Apidae	1	0.10	22	7.44
Halictidae			6	0.87
Clancididae			3	0.44
Formicidae (ant)	189	182.85	388	526.2
Vespidae	20	32.80	11	3.75
Pentatomidae	1	0.09		
Braconidae	1	0.08		
Ni			346	281.2
Lepidoptera				
Tineidae	1	0.08		
Gelechiidae sp.	2	0.17		
Larva	3	0.83		
Sphingidae	1	0,09		
Odonata				
Nayade	1	0.27		
Aeschnidae	26	61.75	21	16.66
Orthoptera				
Grillidae			1	0.07
Grillotalpidae	1	0.26		
Ni	1	0.08		
CRUSTACEA				
Isopoda	2	0.86		
ARACHNIDA				
Araneae	69	189.6	26	14.99
TOTAL	506		974	

Note: Abbreviations: N = number of prey; IRI = index of relative importance; Ni = not identified.

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Jaccard's similarity index comparing the dietary community at the family level between adults and juveniles was 0.78, indicating high similarity. Also, the overlap niche index (Pianka 1973) at the same level showed a 0.64 overlap of dietary communities between adults and juveniles.

Among adults, Hymenoptera (Insecta) was the most numerous prey item (41.8%), followed by Araneae (Arachnida; 13.6%), and Aeglidae (Anomura, Decapoda; 13.4%). Aeglidae was volumetrically the most important trophic item (25.4%), followed by Anura (Amphibia; 25.02%). The highest value of IRI corresponded to Aeglidae (IRI = 811.66) followed by Hymenoptera (IRI = 215.9; Figure 2). In the juveniles, Hymenoptera constituted the highest percentage of prey (77.2%). Aeglidae (IRI = 412.2; Figure 3) had the highest IRI value and was the most important prey volumetrically (87.5%), followed by fishes such as Cyprinodontiformes, Anablepidae, *Jenynsia multidentata* (4.8%) and Characiformes (4.3%).

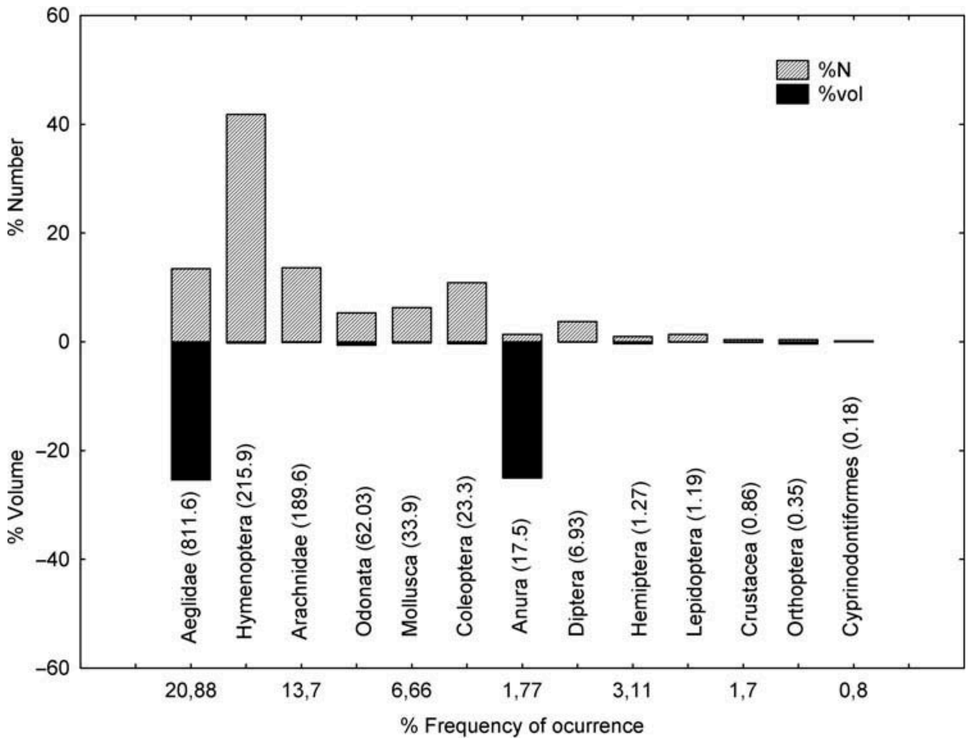

Figure 2. Index of relative importance (IRI) of prey consumed by adult *Lithobates catesbeianus*; % Number (%N) represents the numerical percentage and % volume (%vol) the volumetric percentage, and the horizontal axis represents the frequency of occurrence of each item.

We detected significant correlations between predator size (SVL) and prey size (MLP) in adults (Pearson regression: $R^2 = 0.47$, $P = 0.0001$; MLP = –7.7952 + 0.2787 × SVL) and juveniles (Pearson regression: $R^2 = 0.30$, $P = 0.01$; MLP = –6.5139 + 0.2022 × SVL).

Discussion

Lithobates catesbeianus is considered an opportunistic generalist predator (Korschgen and Baskett 1963; Stebbins and Cohen 1995), and our results agree with these findings. The trophic niche breadth (Levins index) was high for both adults and juveniles. This invasive population consumed a large number of items including 40 taxa in adults and 29 taxa in juveniles, with crabs from the family Aeglidae as the main food item in all frogs. Adults and juveniles of native anurans were recorded in the diet, but in low frequencies. Our results showed that cannibalism in bullfrogs is more common than the consumption of native anurans, coinciding with results reported for other populations of introduced bullfrogs (Wu et al. 2005; Wang et al. 2008). But there is evidence that in introduced bullfrog populations in regions where native amphibian species are abundant, bullfrogs prefer native amphibians as the main item of their diet (Werner et al. 1995; Texeira Da Silva et al. 2009; Boelter et al. 2012). For example, in populations from Brazil with a high abundance of native

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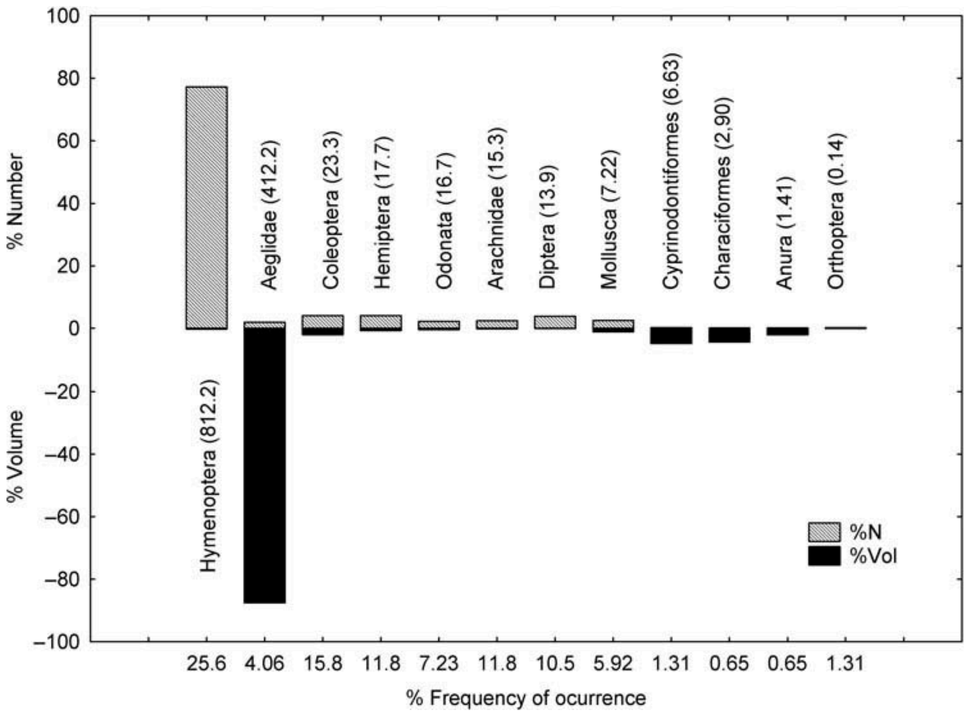

Figure 3. Index of relative importance (IRI) of prey consumed by juvenile *Lithobates catesbeianus*; % Number (%N) represents the numerical percentage and % Volume (%Vol) the volumetric percentage, and the horizontal axis represents the frequency of occurrence of each item.

amphibians, bullfrogs show low cannibalism and ingest more native amphibians (Boelter et al. 2012). For the population studied herein, we think that low predation on native amphibian species (*Rhinella arenarum* and *Leptodactylus latrans*) may be related to the low density of native anurans in these environments compared to the abundance of introduced bullfrogs. Also, predation on the toad *Rhinella arenarum* by bullfrogs is probably deterred by abundant chemical defenses on the skin of *R. arenarum* (Cei et al. 1972). Bullfrogs have been observed to avoid other species of *Rhinella* in South America (Toledo and Jared 1995). Regardless, adult bullfrogs in other introduced populations eat bufonid toads, and Texeira Da Silva et al. (2009) proposed that bullfrogs may have some degree of tolerance to their chemical compounds. Another possibility for the low density of native anurans in that study area is the presence of *Bd* infection from bullfrogs, which are asymptomatic carriers or are sensitive to some strains of *Bd* fungus (Daszak et al. 2003; Gervasi et al. 2013). The bullfrog population studied herein had individuals with positive *Bd* records (Ghirardi 2011), which probably infected populations of *R. arenarum* and *L. latrans* and might have caused a decrease in their population densities. Unfortunately, no information exists about *Bd* infections before the invasion of the bullfrog. More studies are needed to understand the ecological interaction between native and bullfrog populations in this ecosystem.

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We also recorded low consumption of fish (Characiformes and Cyprinodontiformes), which were more abundant in juvenile bullfrogs, similar to what was observed by Wu et al. (2005) in a bullfrog population in China. Low consumption could be the consequence of a shift in microhabitat use through post-metamorphic ontogeny, as suggested by Texeira Da Silva et al. (2009). In our studied population of bullfrogs, juvenile frogs always remained close to the water, as it facilitates their antipredator response (a short call and then a jump into the water).

Dietary similarity (Jaccard index 78%) and overlap niche index (Pianka index 0.64) between adults and juveniles were high. The similarity found in their diets reflects the trophic spectrum of adults (40 taxa) and juveniles (29 taxa) of this bullfrog. Apparently, adults and juveniles eat similar prey categories, but it is clear that the number and size of prey items change between adults and juveniles, probably associated with their body size (Table 3). Large frogs can continue feeding on the same type of prey used by smaller frogs, while also including large prey in their diets (Stebbins and Cohen 1995). The high similarity in the diets of both size classes and the association between the sizes of the predator and prey suggest that the impact caused by bullfrogs throughout their ontogeny is high and probably has an impact on their prey.

Freshwater crabs are the main items in the diet of *L. catesbeianus* in other introduced populations (Tyler and Hoestenbach 1979; Krupa 2002; Hirai 2004; Wu et al. 2005; Wang et al. 2008), and are the most conspicuous prey items (authors' pers. obs.). We observed that *L. catesbeianus* ingested crabs from one species of the family Aeglidae, which is the only crab species endemic to South American rivers (Bond-Buckup et al. 2010). Moreover, it is important to emphasise that crabs were volumetrically the most important item in the diet of both adult and juvenile *L. catesbeianus* in this study population.

The crabs in freshwater ecosystems are part of the lowest trophic level in the food chain (Cumberlidge et al. 2009). In this particular case, it is highly likely that the

Table 3. Morphometric measures (mean ± standard error, SE) and mean volume of prey consumed, as well as other feeding characteristics of each size class, and relationship between size of Bullfrog and MLP in stomach ($R_{Pearson}$; * indicates $P < 0.05$).

	Size classes	
	Adults	Juveniles
Number of individuals	82	87
SVL (mm)	93.5 ± 5.8	58.9 ± 1.6
Weight (g)	125.6 ± 21.9	29.5 ± 4.2
No. of prey	506	972
Mean prey volume	8231.8 ± 2320	3743 ± 1250
TNB	5.3	3.4
Trophic spectrum	40	29
SVL vs MLP	$R^2 = 0.30$*	$R^2 = 0.47$*

Note: SVL = snout-vent length; TNB = trophic niche breadth; MLP = mean length prey in stomachs of Bullfrogs.

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presence of bullfrogs is generating some degree of competition with native species for this food resource (Correia 2001). The major threats to the southern region's freshwater crabs include deforestation, farming and exotic species (Pérez-Losada et al. 2002).

In this paper, we analysed the diet of adult and juvenile bullfrogs, providing the first data on the food habits of this invasive species in an arid environment at mid-elevation in the central Andes of Argentina. We agree with other studies that this bullfrog has a generalist diet with high overlap between adults and juveniles. More studies should be carried out to evaluate whether their impacts extend through the food web.

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