Journal of Zoology. Print ISSN 0952-8369

Anurans as prey: an exploratory analysis and size relationships between predators and their prey

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Keywords
predation; size relationships; allometry; post-metamorphic anurans.

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Received 3 November 2005; accepted 3 May 2006

doi:10.1111/j.1469-7998.2006.00195.x

Abstract

The vertebrate predators of post-metamorphic anurans were quantified and the predator–prey relationship was investigated by analysing the relative size of invertebrate predators and anurans. More than 100 vertebrate predators were identified (in more than 200 reports) and classified as opportunistic, convenience, temporary specialized and specialized predators. Invertebrate predators were classified as solitary non-venomous, venomous and social foragers according to 333 reviewed reports. Each of these categories of invertebrate predators was compared with the relative size of the anurans, showing an increase in the relative size of the prey when predators used special predatory tactics. The number of species and the number of families of anurans that were preyed upon did not vary with the size of the predator, suggesting that prey selection was not arbitrary and that energetic constraints must be involved in this choice. The relatively low predation pressure upon brachycephalids was related to the presence of some defensive strategies of its species. This compounding review can be used as the foundation for future advances in vertebrate predator–prey interactions.

Introduction

Anurans exhibit a great diversity of defensive strategies (e.g. Dodd, 1976), which can include, alone or in combination, ecological, morphological, physiological or behavioural features (Duellman & Trueb, 1994; Toledo & Jared, 1995). The whole defensive repertoire of a population or a species may have evolved due to the strong and continuously selective pressure wielded by its natural predators (Greene, 1997; Vamosi, 2005). Moreover, predators may also have coevolved to suppress these defensive strategies, generating a predator–prey arms race (Brodie & Brodie, 1999*a*,*b*; Geffeney, Brodie & Brodie, 2002). Anurans are known to be preyed upon by so many predators that it has been stated that 'practically anything will eat an amphibian' (Porter, 1972 in Duellman & Trueb, 1994, p. 244). Despite this, there is no data compilation about the actual anuran predators. Most of the reports are anecdotic, reporting just the predation events (see the comments in Toledo, 2005), and few articles make substantial contributions, for example information on predation rates (Olson, 1989; Hinshaw & Sullivan, 1990; Martins, Sazima & Egler, 1993), inferences on the risks of predation (e.g. Ryan, 1985; Haddad & Bastos, 1997) or revising the subject (e.g. McCormick & Polis, 1982; Toledo, 2005).

It is suggested that relatively larger predators generally subdue their prey without using special tactics (Hespenheide, 1973). On the other hand, in order to capture larger or equal-sized prey, it is possible that predators make use of specialized tactics such as poisoning, trapping or social foraging (Hespenheide, 1973; McCormick & Polis, 1982; McNab, 1983; Pough, Heiser & McFarland, 1990; Menin, Rodrigues & Azevedo, 2005). Again, these theories have not been tested jointly for anurans. Therefore, in the present study we carried out a qualified and quantified review of the main vertebrate predators of post-metamorphic anurans, verifying the relationship between relative predator–prey sizes. We have also considered the use of specialized predation tactics in relation to relative size of prey.

Methods

Vertebrate predators

Given the large number of available reports on post-metamorphic anurans as prey of vertebrates (invertebrate predators have been reviewed elsewhere: Toledo, 2005), only unpublished data, articles and natural history notes published in *Herpetological Review* (since the first number in the late 1960s up to the last number of 2005) were considered. Additional references were only considered when they provided relative significant contributions, for example when referring to an unreported family (or even a higher taxa) of prey and/or predator. Furthermore, we only considered articles that identified both prey (anurans) and predators (vertebrates) to the specific level. Predation

attempts in the field, laboratory experiments and captivity observations were also not considered. Specific names are in agreement with online databases: amphibians follow Frost (2004) complemented by Faivovich *et al.* (2005), Nascimento, Caramaschi & Cruz (2005) and Frost *et al.* (2006), reptiles follow Uetz *et al.* (2005), fishes follow Froese & Pauly (2004), birds follow Lepage (2005) and mammals follow Wilson & Reeder (1993).

To assert that our review is representative over the anuran phylogenetic groups, we performed linear regression analysis between number of species in the family and number of predation reports, including data from invertebrates (based on Toledo, 2005) and vertebrates (present study), and expected to find a positive significance fixing α in 99%. The statistical outlier was determined after residual analysis (Zar, 1999).

Size relationships and predation tactics

The predator–prey size relationship was verified from the analysis of 333 accounts of invertebrate predation upon anurans (see table 2 in Toledo, 2005), taking into account the relative size of the prey in relation to predators [R_s = snout–vent length (SVL) of anuran/total length (TL) of invertebrate] and the presence or absence of specialized predatory tactics, such as use of traps (e.g. webs), poison, social foraging or any association between them. Values of R_s are presented as mean $\pm$ SD (range). Vertebrate predators were not included in this analysis because, in the majority of cases, they were many times larger than anurans, complicating the visualization of the results (see the Discussion).

For R_s comparisons among predator groups, a Mann–Whitney (t) test was used. Predator size was correlated with anuran size using linear correlation. The same analysis was used when correlating the size classes of the invertebrates and the number of families of anurans that were preyed upon. Values were considered significant when $P \leq 0.001$.

Results

Our databases, including invertebrate and vertebrate predators, comprised 21 anuran families. We found a positive relation between species of anurans in the families and number of reports of predation (adjusted $r^2 = 0.41$; $F = 14.41$; $P = 0.001$; $n = 21$; Fig. 1). The only group found to be an outlier was the family Brachycephalidae. Out of the 95% confidence interval were the Leiopelmatidae, Leptodactylidae, Microhylidae, Pipidae, Racophoridae and Scaphiopodidae families. Among these families, Microhylidae was differentiated the most (Fig. 1).

Vertebrate predators

More than 100 anuran species ($n = 137$), belonging to 16 families (Brachycephalidae, Bufonidae, Ceratophryidae, Cycloramphidae, Dendrobatidae, Dicroglossidae, Hylidae, Leiopelmatidae, Leptodactylidae, Mantellidae, Megophryidae, Microhylidae, Pipidae, Pyxicephalidae, Ranidae and Scaphiopodidae), were reported as prey of 136 species from

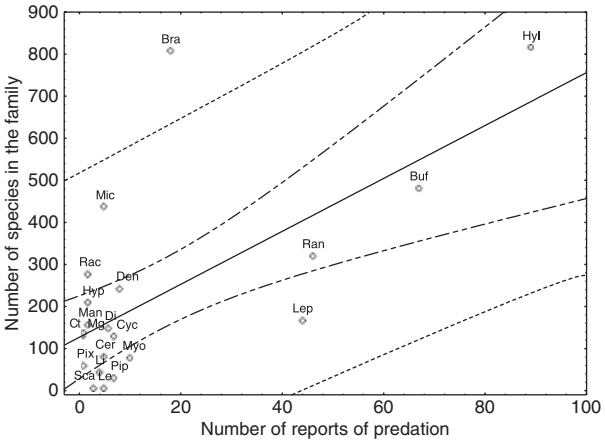

Figure 1 Linear regression, 95% confidence interval and 95% prediction interval ellipse between the number of reports of predation by invertebrates and vertebrates upon post-metamorphic anurans and the number of species in anuran families. The labels refer to the names of the families: Brachycephalidae (Bra), Bufonidae (Buf), Cetratophryidae (Cer), Centrolenidae (Ct), Cycloramphidae (Cyc), Dendrobatidae (Den), Dicroglossidae (Di), Hylidae (Hyl), Hyperoliidae (Hyp), Leptodactylidae (Lep), Leiopelmatidae (Le), Limnodynastidae (Li), Mantellidae (Man), Megophryidae (Mg), Microhylidae (Mic), Myobatrachidae (Myo), Pipidae (Pip), Pyxicephalidae (Pix), Ranidae (Ran), Racophoridae (Rac) and Scaphiopodidae (Sca).

all the main groups of vertebrates (Osteichthyes, Amphibia, Reptilia, Aves and Mammalia; Fig. 2; Supplementary Material Appendix S1). Among them, snakes were the most representative group, being referred to in about 45% of the reports (Fig. 3).

We were able to divide vertebrate predators into four categories:

(1) Opportunistic predators: those who feed on anurans occasionally and opportunistically. These predators are diet-generalist and prey on anurans when, once in a while, they encounter them in nature. This is the largest group and made up about 42% of the reports, and is formed by fishes, salamanders, turtles, lizards, crocodilians and some species of birds and mammals (see also Poulin *et al.*, 2001; Bueno, Belentani & Motta-Junior, 2002; Seamark & Bogdanowicz, 2002; Fig. 2).

(2) Convenience predators: they are not predators specialized on anurans, but feed on them with regularity. In this case, the most representative predators are those who exhibit similar habits to the anurans, facilitating their (predator–prey) encounters. Examples are the anurans themselves (about 25% of the reports; Fig. 2) and some bird species (e.g. *Geranospiza caerulescens*) that forage in areas where the chances of encountering anurans is greatly enhanced, such as margins of water bodies, gaps on tree trunks, axils of bromeliads and holes in the ground (e.g. Bokermann, 1978).

(3) Temporary specialized predators: those who look specifically for anurans in a determined phase of their life cycle or for a determined purpose. In this case we included some

Figure 2 Post-metamorphic anurans preyed upon by vertebrates: (a) adult *Leptodactylus* cf. *ocellatus* preying upon a conspecific juvenile; (b) adult *Liophis miliaris* preying upon an adult male *Hypsiboas faber*; (c) a *Callithrix penicillata* eating an adult *Hypsiboas lundii*; and (d) an adult *Trogon surrucura* preying upon an adult *Hypsiboas albomarginatus*.

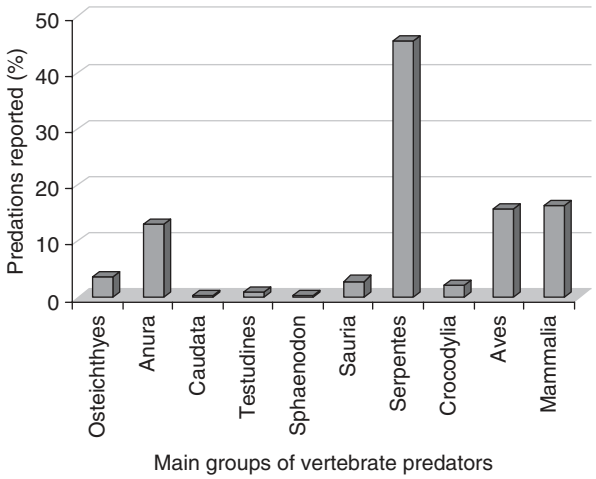

Figure 3 Percentage of the main vertebrate groups reported as post-metamorphic anuran predators (data source: Supplementary Material Appendix S1; $n = 243$).

snakes, such as some species of *Bothrops* that feed exclusively or primarily on anurans when they are juveniles (Sazima, 1992; Hartmann, Hartmann & Giasson, 2003; Nogueira, Sawaya & Martins, 2003). Another example are some bird species, for example *Trogon surrucura* and *Pitangus sulphuratus*, that hunt for anurans to feed their nestlings (Toledo *et al*., 2005; Fig. 2) or males of *Baryphthengus martii* that provide colourful anurans (dendrobatids) to females as a courtship signal (Master, 1999). A third possibility in this group is represented by those vertebrates that prey upon anurans in order to use their skin toxins in their own defence (Brodie, 1977). This is the smallest group, making up less than 1% of the reports.

(4) Specialized predators: this group is basically formed by some bat species, for example *Cardioderma cor* and *Megaderma* spp., but mainly *Trachops cirrhosus* (Tuttle, Taft & Ryan, 1982; Tandler, Phillips & Nagato, 1996), and several snake species specialized in hunting anurans, for example *Chironius* spp. and *Liophis* spp. (Duellman, 1978; Michaud & Dixon, 1989; Martins & Oliveira, 1999; Marques, Eterovick & Endo, 2001; Fig. 2). Indeed, some snake species exhibit preferences, occasionally together with morphological specializations, for hunting species within a genus or a family. For example, the snakes *Causus rhombeatus*, *Waglerophis merremi* and *Xenodon newiedii* are specialized in hunting *Chaunus* spp. or other bufonids that they may face (Vanzolini, Ramos-Costa & Vitt, 1980; Duellman & Trueb, 1994; Marques *et al*., 2001). This category comprises *c*. 31% of the reports.

Size relationships and predation tactics

In all reported predation events, vertebrate predators were larger than anurans. Anurans were preyed upon even when they had a large amount of skin toxins (e.g. bufonids, *Leptodactylus labyrinthicus* and *Leptodactylus pentadactylus*) or highly toxic skin secretions (e.g. *Atelopus varius*, *Dendrobates auratus, Eupemphix nattereri* and *Phyllobates terribilis*; Supplementary Material Appendix S1).

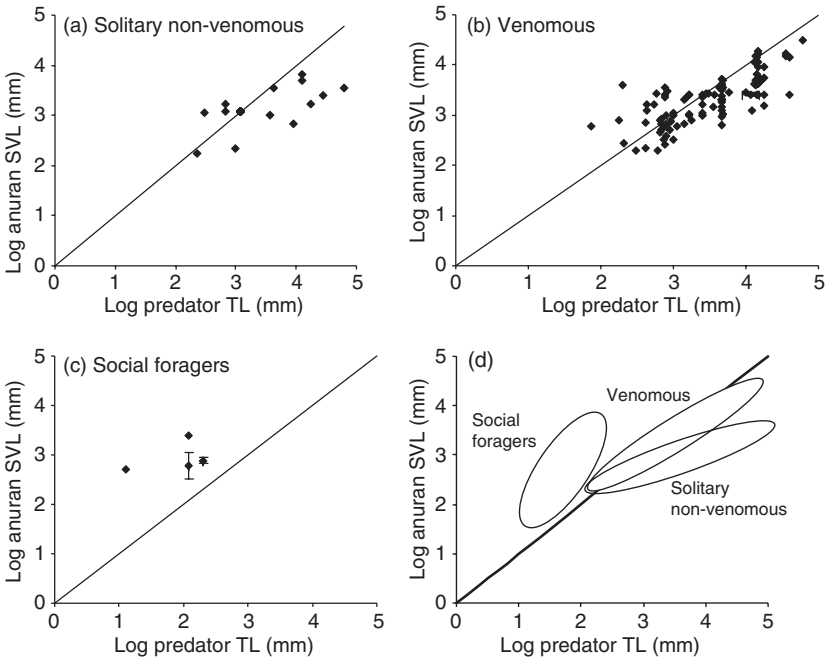

Figure 4 Relationship between anuran snout–vent length (SVL) and the total length (TL) of their respective invertebrate predators (data from Toledo, 2005). Predators are divided into the following categories: (a) solitary non-venomous ($n=34$), (b) venomous ($n=132$) and (c) social foragers ($n=167$). (d) A schematic synthesis of the relationships among all categories of invertebrate predator sizes and anuran sizes.

Of the 333 reported predations by invertebrates upon post-metamorphic anurans, 34 were made by predators that did not use specialized tactics [$R_s = 0.92 \pm 0.31$ (0.29–1.78)] and 299 by predators with specialized tactics [$R_s = 1.52 \pm 0.79$ (0.30–5.00)]. These groups differed significantly between their R_s values ($t = 3585.5$; $P < 0.0001$), suggesting that when the invertebrates exhibited specialized tactics they were practically the same size as their prey (venomous predators) or smaller than their prey (social foragers). On the other hand, when they were solitary non-venomous predators, they were relatively larger than their prey (Fig. 4).

Only 34.11% of the invertebrates were larger than their victims. The SVL of the anurans was positively correlated with the TL of the solitary non-venomous ($r = 0.64$; $P < 0.001$; $n = 34$) and venomous predators ($r = 0.78$; $P < 0.001$; $n = 132$), but not with the social foragers ($r = 0.13$; $P = 0.08$; $n = 167$). Excluding the social foragers, the larger the invertebrate, the smaller the relative size of the captured prey (Fig. 4). We did not find a significant correlation between TL categories and the number of families of anurans ($r = -0.09$; $P = 0.83$; $n = 8$) or the number of species that were preyed upon ($r = -0.41$; $P = 0.31$; $n = 8$; Table 1).

Table 1 Invertebrate total length (TL) classes and the respective number of anuran families and species that were preyed upon

TL classes in mm (n)	Number of anuran families	Number of anuran species
3–10 (172)	3	8
11–20 (32)	5	20
21–30 (36)	5	13
31–40 (30)	6	15
41–50 (4)	2	2
51–60 (15)	3	6
61–70 (35)	6	13
85–200 (9)	3	6

Discussion

Size relationships and predation tactics

McCormick & Polis (1982) observed, to a certain extent, a similar proportion (45%; $n = 134$) of invertebrate predators that were larger than their vertebrate prey compared with that calculated in the present study (34%; $n = 333$). Besides this, in accordance with our observations, an increase in relative prey size with sociality level of the predator has also been reported (for invertebrates, see McCormick & Polis, 1982; for vertebrates, see McNab, 1983). Coincident observations among different predators and prey groups (from small invertebrates to large vertebrates) suggest that these relationships must be widespread in natural communities.

Without considering social foragers, we observed that the larger the invertebrate predator, the smaller the relative prey size. This fact can be related to an ontogenetic variation in the diet of invertebrates (e.g. Cisneros & Rosenheim, 1997; Koperski, 1997), which could be focused on more energetically valuable items in terms of accessibility and/or subjugation facility (MacArthur & Pianka, 1966; Bennett, 1986). That is, the larger the anuran, the larger its capacity to escape from a predator (Formanowicz *et al.*, 1981). Therefore, these predators would have a higher energetic cost implied for searching, stalking, striking and subduing (including killing and ingesting) relatively larger prey. Another possibility would be an alteration in the encounter rate of predators and prey in the wild because of differences of habits and density among classes of size of both

invertebrates and anurans (MacArthur & Pianka, 1966). Therefore, it would be more advantageous, in energetic terms, to hunt for relatively smaller (Enders, 1975) and/or more accessible prey (Begon, Harper & Townsend, 1990). Nonetheless, the larger the anuran, the lower the risk of invertebrate predation (present study), and at a certain moment the anuran can become the predator of the invertebrate (see the Discussion).

Vertebrate predators were not included in this analysis; however, their inclusion would only reinforce our correlations and comparisons because vertebrates that prey on anurans are many times larger than their prey, are solitary hunters, and do not use traps or poison (with the exception of venomous snakes).

For hunting prey that are larger than they are, predators are commonly reported to make use of specialized tactics (Hespenheide, 1973; Enders, 1975; McCormick & Polis, 1982; present study). However, this does not exclude the availability of relatively smaller prey to these predators (Enders, 1975). Consequently, predators that use these tactics may capture a broader array of prey (with regard to size) when compared with solitary non-venomous predators. Consecutively, it is possible that an increase in the amplitude of prey sizes could allow a diversification (with regard to richness) of items that could be captured. However, our results do not sustain these hypotheses, that is we observed neither an increase in the amplitude of sizes of anurans that were captured (Fig. 4b and c) nor an increase in the richness of dietary items (Table 1) with the increment of predator body size (length). Therefore, we suggest that invertebrates could be selecting their prey because of energetic restrictions involved in the predatory process of searching, stalking, striking or subduing (including killing and ingesting; e.g. Brooks & Dodson, 1965; Griffiths, 1975, 1980; Bennett, 1986).

Predators and defence

Studying snakes and their predators, Greene (1997) suggested that, because endothermic predators (birds and mammals) have higher metabolic rates than ectothermic ones (Randall *et al*., 2002), endothermic predators must ingest their prey at a higher rate. Therefore, birds and mammals must input a greater selective pressure over defensive strategies than ectothermic predators (such as snakes). Even though it could be true for anurans and their predators (it has never been tested), another factor must be considered in this relation. Although snakes do not feed at the same rate as endotherms, for example a single adult hawk is able to eat up to 18 adult anurans in a 4 h period (Bokermann, 1978), there is a much larger number of species and individuals (independent of the species) of snakes that hunt occasionally, preferentially or specifically for anurans. In contrast, birds and mammals are occasional predators, usually much more generalist (present study). Hence, if the relative abundance of snakes is higher than that of other predators (e.g. birds and mammals), in a determined area and in a determined time (the relative abundance of a predator group varies within latitudinal ranges and within biomes; Greene, 1988), snakes should be considered the main anuran predators. As a consequence, it is possible that snakes have been (or are) driving the diversification of anuran defensive strategies (see the discussion in Vamosi, 2005). Similarly, spiders may play a significant role if invertebrates are taken into account (see Toledo, 2005).

Another aspect that seems to influence the divergence and maintenance of specific defensive behaviour is the success in escaping from predators (Greene, 1988). That is, predators that have commonly hunted anuran species, except anurans who present successful defences, are those driving the evolution of such mechanisms (Greene, 1988). This hypothesis is intuitive when considering anuran communities, because we have few experimental and field approaches that corroborate or reject it (e.g. Formanowicz *et al*., 1981; Heinen, 1995; Heinen & Hammond, 1997; Leary & Razafindratsita, 1998). However, if this is true for anurans, not all snake and spider species are those driving the evolution of defensive mechanisms in anurans, but only some of them or even another group of species. All these suggestions still need clarification by means of field observations, experimentation and broader analysis.

Most of the *Eleutherodactylus* and *Craugastor* species (which represents the majority of the species in the family Brachycephalidae) occur spread on the forest floor (L. F. Toledo *et al*., pers. obs.), have cryptic colorations and are very polymorphic (Hoffman & Blouin, 2000; Sander *et al*., 2003). In contrast, aposematic and toxic *Brachycephalus* species can be found in very high densities distributed in a patch pattern on the forest floor. Some of the cryptic species of *Brachycephalus*, such as *Brachycephalus nodoterga*, can be found spread on the forest floor like *Eleutherodactylus* spp. and *Craugastor* spp. (L. F. Toledo *et al*., pers. obs.). Hence, these morpho-ecological characteristics may efficiently prevent individuals of this family from being preyed upon. However, we do not exclude the possibility of their cryptic and distributional characteristics to difficult field observations of predation. Microhylids were also preyed upon less than expected. Most microhylids are fossorial and explosive breeders, emerging from their galleries a few days a year (Duellman & Trueb, 1994). Therefore, this would again explain the few numbers of predation accounts. The scenery for the other families that were not included in the confidence interval may change with additional predation reports and species descriptions.

Cross predation, cannibalism and threats

Although anurans are preyed upon by practically any kind of animal, we observed countless reports that lead us to suggest status inversion, that is from being prey they become predators when the size relationship becomes more favourable for the anurans. Stomach content studies provide many examples of anurans feeding primarily on small invertebrates (Pough *et al*., 1998). Nevertheless, large-sized anurans, such as *Conraua goliath*, *Ceratophrys*, some *Leptodactylus*, *Pyxicephalus* and *Lithobates* spp., can prey upon

several types of vertebrates (Duellman & Trueb, 1994). *Lithobates catesbeianus*, for example, has already been reported feeding on fish (Cross & Gerstenberger, 2002), turtles (Graham, 1984), snakes (Carpenter, Casazza & Wylie, 2002; Rorabaugh & Humphrey, 2002), birds (Black, 1974), bats (Kirkpatrick, 1982), mice, minks (Beringer & Johnson, 1995) and other anurans, including conspecific individuals (references in Supplementary Material Appendix S1). Cannibalism is reported essentially among species of *Lithobates* (Stuart & Painter, 1993; Rombough, Jordan & Pearl, 2003; Supplementary Material Appendix S1), yet there is no evidence that conspecifics are able to recognize themselves, cannibalism being only an opportunistic form of predation (Duellman & Trueb, 1994). In this way, alien populations of *Li. catesbeianus*, introduced generally by frog farms, represent a strong threat to native vertebrate populations, but primarily for anuran populations (Batista, 2002; Borges-Martins & Di-Bernardo, 2002; Kats & Ferrer, 2003), because they are highly voracious convenience predators (*sensu* present study).

Another important anuran predator is the human being. Although the effects of hunting are relatively unknown, there is evidence of human impact over some populations or species (Schlaepfer, Hoover & Dodd, 2005), leading some of them to noticeable decline or even to extinction (Beebee, 1996; Collins & Storfer, 2003). Humans hunt for anurans essentially with three objectives: for (1) exhibitions and pets, (2) science or education and (3) skin and meat supply. The latter is most intense for large anurans, occurs all over the world and should be the most impacting (Beebee, 1996). As examples of species that have been hunted for human feeding, we can list *Co. goliath* (Africa), *Rana draytonii*, *Li. catesbeianus* (North America), *Leptodactylus fallax*, *Le. labyrinthicus*, *Le. ocellatus*, *Le. pentadactylus* (Central and South America), *Hoplobatrachus rugulosus* (Asia) and *Rana temporaria* (Europe) (Beebee, 1996; Collins & Storfer, 2003; AmphibiaWeb, 2005; Zina & Haddad, 2005; L. F. Toledo & C. F. B. Haddad, unpubl. data).

Finally, we believe that our study, rather than a closing review of the subject, must be considered a starting point for future research clarifying several aspects of the natural history of vertebrates (especially anurans), mainly aspects related to predation, defence and conservation. Our results may also help in studies of communities of predators, especially those involving size relationship analyses.

Acknowledgements

We thank Anne d'Heursel and Cynthia Prado for discussing earlier drafts of the manuscript; Harry W. Greene for reviewing and making valuable comments on the manuscript; Rogério P. Bastos for providing unpublished data; Rodrigo Lingnau for providing some old references; Christine Strüssmann, Marcio Martins, Gustavo Canale and Germano Woehl Jr. for providing pictures of *Leptodactylus* cf. *ocellatus*, *Hypsiboas faber*, *Hypsiboas lundii* and *Hypsiboas albomarginatus*, respectively; FAPESP (BIOTA proc. no. 01/13341-3) and CNPq for grants to the Herpetology Lab; CAPES and CNPq for scholarships; and Idea Wild and Neotropical Grassland Conservancy for the donation of equipment.

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Supplementary material

The following material is available for this article online:

Appendix S1 Vertebrate predators (136 species; 50 families) and their respective prey: post-metamorphic anurans (137 species; 16 families) reviewed from 243 reports (including unpublished observations).

This material is available as part of the online article from http://www.blackwell-synergy.com

Appendix I. Vertebrate predators (136 species; 50 families) and their respective prey: post-metamorphic anurans (137 species; 16 families) reviewed from 243 reports (including unpublished observations).

Vertebrate Predator		Anuran Prey		Reference
Higher Taxa	species	Family	species	
Osteichthyes				
Anguillidae	*Anguilla reinhardtii*	Hylidae	*Litoria lesueurii*	Harvey *et al*., 1999
Centrarchidae	*Lepomis cyanellus*	Hylidae	*Pseudacris cadaverina*	Ervin *et al*., 2000
	Micropterus salmoides	Hylidae	*Pseudacris cadaverina*	Hovey & Ervin, 2005
	Micropterus salmoides	Ranidae	*Lithobates pipiens*	Cochran, 1982
	Micropterus salmoides	Ranidae	*Lithobates sylvaticus*	Cochran, 1999
Characidae	*Brycon guatemalensis*	Dendrobatidae	*Dendrobates auratus*	Hedstrom & Bolaños, 1986
Erythrinidae	*Hoplias* cf. *malabaricus*	Bufonidae	*Chaunus ornatus*	Haddad & Bastos, 1997
Salmonidae	*Salmo trutta*	Hylidae	*Pseudacris crucifer*	Cochran & Cochran, 2003
	Salmo trutta	Ranidae	*Rana cascadae*	Simons, 1998
Amphibia				
Anura				
Bufonidae	*Anaxyrus terrestris*	Ranidae	*Lithobates heckscheri*	Beane & Pusser, 2005
	Chaunus jimi	Bufonidae	*Chaunus granulosus*	Guix, 1993
Ceratophryidae	*Ceratophrys aurita*	Bufonidae	*Chaunus scheneideri*	R. P. Bastos, unpubl. data
	Ceratophrys cranwelli	Leptodactylidae	*Physalaemus biligonigerus*	Wild, 2001
	Ceratophrys cranwelli	Microhylidae	*Dermatonotus muelleri*	Wild, 2001
Hylidae	*Hypsiboas faber*	Hylidae	*Scinax granulatus*	Solé *et al*., 2004
Leptodactylidae	*Leptodactylus labyrinthicus*	Hylidae	*Hypsiboas albopunctatus*	L. F. Toledo & O. G. S. Araújo, unpubl. data
	Leptodactylus labyrinthicus	Hylidae	*Hypsiboas faber*	C. F. B. Haddad, unpubl. data
	Leptodactylus labyrinthicus	Leptodactylidae	*Eupemphix nattereri*	Silva *et al*., 2003
	Leptodactylus ocellatus	Hylidae	*Hypsiboas albomarginatus*	C. F. B. Haddad, unpubl. data
	Leptodactylus ocellatus	Hylidae	*Hypsiboas faber*	Haddad & Sazima, 1992
	Leptodactylus ocellatus	Leptodactylidae	*Leptodactylus ocellatus*	Kokubum & Rodrigues, 2005
	Leptodactylus ocellatus	Leptodactylidae	*Eupemphix nattereri*	Rodrigues & Filho, 2004
	Leptodactylus pentadactylus	Leptodactylidae	*Hypsiboas rosenbergi*	Kluge, 1981
	Leptodactylus podicipinus	Bufonidae	*Chaunus granulosus*	Guimarães *et al*., 2004
	Litoria aurea	Leiopelmatidae	*Leiopelma archeyi*	Thurley & Bell, 1994
Ranidae	*Ptychadena mascareniensis*	Mantellidae	*Mantidactylus wittei*	McIntyre & Ramanamanjato, 1999
	Rana aurora	Hylidae	*Pseudacris regilla*	Arnold & Halliday, 1986

	Lithobates blairi	Hylidae	*Pseudacris triseriata*	Bolek & Janvy Jr., 2004
	Rana cascade	Ranidae	*Rana cascadae*	Rombough *et al*., 2003
	Lithobates catesbeianus	Bufonidae	*Anaxyrus californicus*	Griffin & Case, 2002
	Lithobates catesbeianus	Bufonidae	*Anaxyrus fowleri*	Smith & Green, 2002
	Lithobates catesbeianus	Bufonidae	*Anaxyrus nelsoni*	Jones *et al*., 2003
	Lithobates catesbeianus	Hylidae	*Pseudacris triseriata*	Bolek & Janvy Jr., 2004
	Lithobates catesbeianus	Ranidae	*Rana aurora*	Cook, 2002
	Lithobates catesbeianus	Ranidae	*Rana boylii*	Crayon, 1998
	Lithobates catesbeianus	Ranidae	*Lithobates catesbeianus*	Stuart & Painter, 1993
	Lithobates catesbeianus	Scaphiopodidae	*Scaphiopus hammondi*	Hays & Warner, 1985
	Rana luteiventris	Bufonidae	*Anaxyrus boreas*	Pearl, 2000
	Rana luteiventris	Ranidae	*Rana luteiventris*	Pilliod, 1999
	Rana pretiosa	Ranidae	*Rana pretiosa*	Pilliod, 1999
	Lithobates vaillanti	Hylidae	*Agalychnis callidryas*	Vaughan, 2003
Caudata				
Ambystomatidae	*Dicamptodon copei*	Leiopelmatidae	*Ascaphus truei*	Aresco & Reed, 1998
Reptilia				
Crocodylia				
Alligatorinae	*Caiman crocodilus*	Bufonidae	*Chaunus granulosus*	Gorzula, 1977
	Caiman crocodilus	Leptodactylidae	*Pleuroderma brachyops*	Gorzula, 1977
	Caiman crocodilus	Microhylidae	*Elachistocleis ovalis*	Gorzula, 1977
	Caiman yacare	Hylidae	*Pseudis paradoxa*	Santos *et al*. 1996
	Paleosuchus palpebrosus	Bufonidae	*Chaunus scheneideri*	L. F. Toledo, unpubl. data
Rynchocephalia				
Sphenodontidae	*Sphenodon punctatus*	Leiopelmatidae	*Leiopelma hamiltoni*	Newman, 1977
Sauria				
Gekkonidae	*Thecadactylus rapicauda*	Brachycephalidae	*Eleutherodactylus johnstonei*	Henderson & Berg, 2005
Gerrhosauridae	*Zonosaurus madagascariensis*	Mantellidae	*Mantella laevigata*	Heying, 2001
Teiidae	*Ameiva festiva*	Leptodactylidae	*Leptodactylus poecilochilus*	Toral, 2004
	Crocodilus amazonicus	Bufonidae	*Chaunus marinus*	Costa *et al.*, 2005
	Tupinambis merianae	Leptodactylidae	*Leptodactylus ocellatus*	Silva & Hillesheim, 2004
	Tupinambis merianae	Bufonidae	*Chaunus schneideri*	L. F. Toledo, unpubl. data
	Tupinambis teguixim	Leptodactylidae	*Leptodactylus mystaceus*	Souza *et al*., 2002

Serpentes				
Boidae	*Boiga irregularis*	Bufonidae	*Chaunus marinus*	Caudell *et al*., 2000
Colubridae	*Alsophis portoricensis*	Brachycephalidae	*Eleutherodactylus antillensis*	Rodríguez-Robles & Leal, 1993
	Alsophis portoricensis	Brachycephalidae	*Eleutherodactylus coqui*	Rodríguez-Robles & Leal, 1993
	Antillophis andreae	Bufonidae	*Peltophryne peltocephalus*	Fong, 2004
	Antillophis andreae	Brachycephalidae	*Euhyas dimidiatus*	Fong, 2004
	Chironius exoletus	Hylidae	*Phyllomedusa distincta*	Castanho, 1996
	Chironius multiventris	Hylidae	*Bokermannohyla circumdata*	Rocha *et al*., 1999
	Chironius multiventris	Cycloramphidae	*Proceratophrys appendiculata*	Rocha *et al*., 1999
	Clelia bicolor	Hylidae	*Trachycephalus venulosus*	Prado, 2003
	Dendrelaphis pictus	Dicroglossidae	*Ferjevaria limnocharis*	Pauwels, 2002
	Enhydris plumbea	Dicroglossidae	*Ferjevaria limnocharis*	Pauwels, 2002
	Helicops angulatus	Hylidae	*Hypsiboas crepitans*	Silva Jr. *et al*., 2003
	Helicops infrataeniatus	Hylidae	*Phyllomedusa iheringii*	Feltrim & Cechin, 2000
	Helicops infrataeniatus	Leptodactylidae	*Eupemphix nattereri*	Martins & Duarte, 2003
	Heterodon platirhinos	Bufonidae	*Anaxyrus fowleri*	Tucker, 2000
	Heterodon platirhinos	Ranidae	*Lithobates pipiens*	Bakkegard & Greene, 2002
	Leimadophis epinephelus	Dendrobatidae	*Phyllobates terribilis*	Myers *et al.*, 1978.
	Leptodeira annulata	Hylidae	*Hypsiboas rosenbergi*	Kluge, 1981
	Leptodeira annulata	Ranidae	*Lithobates vaillanti*	Mora, 1999
	Leptodeira septentrionalis	Hylidae	*Scinax elaeochroa*	Russell *et al*., 1999
	Leptophis ahaetulla	Hylidae	*Trachycephalus venulosus*	Albuquerque & Di-Bernardo, 2005
	Leptophis ahaetulla	Hylidae	*Dendropsophus nanus*	Lopez *et al*., 2003
	Leptophis ahaetulla	Hylidae	*Scinax* cf. *acuminatus*	Lopez *et al*., 2003
	Leptophis ahaetulla	Hylidae	*Scinax nasicus*	Lopez *et al*., 2003
	Liophis anomalus	Bufonidae	*Chaunus arenarum*	Michaud & Dixon, 1989
	Liophis anomalus	Bufonidae	*Chaunus dorbignyi*	Michaud & Dixon, 1989
	Liophis anomalus	Bufonidae	*Chaunus granulosus*	Michaud & Dixon, 1989
	Liophis anomalus	Ceratophryidae	*Ceratophrys ornata*	Michaud & Dixon, 1989
	Liophis anomalus	Leptodactylidae	*Leptodactylus ocellatus*	Michaud & Dixon, 1989
	Liophis cobella	Dendrobatidae	*Mannophryne trinitatis*	Michaud & Dixon, 1989
	Liophis dilepis	Leptodactylidae	*Leptodactylus fuscus*	Michaud & Dixon, 1989
	Liophis dilepis	Leptodactylidae	*Leptodactylus ocellatus*	Michaud & Dixon, 1989
	Liophis dilepis	Leptodactylidae	*Physalaemus cuvieri*	Michaud & Dixon, 1989

Liophis epinephelus	Bufonidae	*Atelopus varius*	Greene, 1997
Liophis epinephelus	Bufonidae	*Chaunus marinus*	Michaud & Dixon, 1989
Liophis epinephelus	Bufonidae	*Rhinella margaritifera*	Michaud & Dixon, 1989
Liophis epinephelus	Brachycephalidae	*Craugastor fitzingeri*	Michaud & Dixon, 1989
Liophis lineatus	Hylidae	*Scinax ruber*	Michaud & Dixon, 1989
Liophis lineatus	Leptodactylidae	*Leptodactylus fuscus*	Michaud & Dixon, 1989
Liophis melanotus	Bufonidae	*Chaunus granulosus*	Michaud & Dixon, 1989
Liophis meridionalis	Leptodactylidae	*Leptodactylus fuscus*	Kokubum & Giaretta, 2002
Liophis miliaris	Bufonidae	*Chaunus granulosus*	Michaud & Dixon, 1989
Liophis miliaris	Leptodactylidae	*Leptodactylus ocellatus*	Michaud & Dixon, 1989
Liophis miliaris	Microhylidae	*Elachistocleis bicolor*	Michaud & Dixon, 1989
Liophis miliaris	Pipidae	*Pipa carvalhoi*	Michaud & Dixon, 1989
Liophis poecilogyrus	Bufonidae	*Chaunus arenarum*	Michaud & Dixon, 1989
Liophis poecilogyrus	Bufonidae	*Chaunus dorbignyi*	Michaud & Dixon, 1989
Liophis poecilogyrus	Bufonidae	*Chaunus granulosus*	Michaud & Dixon, 1989
Liophis poecilogyrus	Hylidae	*Hypsiboas multifasciatus*	Silva Jr. *et al*., 2003
Liophis poecilogyrus	Hylidae	*Hypsiboas pulchellus*	Michaud & Dixon, 1989
Liophis poecilogyrus	Hylidae	*Trachycephalus venulosus*	Silva Jr. *et al*., 2003
Liophis poecilogyrus	Hylidae	*Scinax ruber*	Michaud & Dixon, 1989
Liophis poecilogyrus	Leptodactylidae	*Leptodactylus ocellatus*	Michaud & Dixon, 1989
Liophis poecilogyrus	Leptodactylidae	*Leptodactylus ocellatus*	Michaud & Dixon, 1989
Liophis poecilogyrus	Cycloramphidae	*Odontoprhynus americanus*	Michaud & Dixon, 1989
Liophis poecilogyrus	Leptodactylidae	*Physalaemus cuvieri*	Michaud & Dixon, 1989
Liophis poecilogyrus	Leptodactylidae	*Physalaemus fernandezae*	Michaud & Dixon, 1989
Liophis poecilogyrus	Leptodactylidae	*Physalaemus gracilis*	Michaud & Dixon, 1989
Liophis poecilogyrus	Pipidae	*Pipa carvalhoi*	Michaud & Dixon, 1989
Liophis reginae	Bufonidae	*Rhinella margaritifera*	Michaud & Dixon, 1989
Liophis reginae	Dendrobatidae	*Mannophryne trinitatis*	Michaud & Dixon, 1989
Liophis reginae	Hylidae	*Scinax ruber*	Michaud & Dixon, 1989
Liophis reginae	Brachycephalidae	*Craugastor biporcatus*	Michaud & Dixon, 1989
Liophis reginae	Brachycephalidae	*Eleutherodactylus terraebolivaris*	Michaud & Dixon, 1989
Liophis reginae	Leptodactylidae	*Leptodactylus wagneri*	Michaud & Dixon, 1989
Liophis sagittifer	Leptodactylidae	*Leptodactylus ocellatus*	Michaud & Dixon, 1989
Liophis typhlus	Leptodactylidae	*Leptodactylus mystacinus*	Michaud & Dixon, 1989

Liophis viridis	Hylidae	*Scinax ruber*	Michaud & Dixon, 1989
Liophis viridis	Leptodactylidae	*Physalaemus cuvieri*	Michaud & Dixon, 1989
Masticophis flagellum	Scaphiopodidae	*Scaphiopus couchii*	Ryberg & Dayton, 2004
Nerodia fasciata	Ranidae	*Lithobates capito*	Jensen, 2000
Nerodia fasciata	Scaphiopodidae	*Scaphiopus holbrookii*	Palis, 2000
Nerodia valida	Bufonidae	*Anaxyrus punctatus*	Blazquez, 1996
Philodryas patagoniensis	Bufonidae	*Chaunus granulosus*	Lopez, 2003
Philodryas patagoniensis	Leptodactylidae	*Leptodactylus gracilis*	Lopez, 2003
Pliocercus euryzonus	Brachycephalidae	*Eleutherodactylus* sp.	Greene, 1997
Ptyas korros	Dicroglossidae	*Fejervaria limnocharis*	Pauwels, 2002
Rhabdophis murudensis	Megophrydae	*Megophrys kobayashii*	Das & Tuen, 2005
Thamnodynastes strigatus	Hylidae	*Dendropsophus minutus*	C. F. B. Haddad, unpubl. data
Thamnodynastes strigatus	Hylidae	*Hypsiboas faber*	Souza *et al*., 2003
Thamnodynastes strigatus	Cycloramphidae	*Crossodactylus* cf. *bokermanni*	Kopp & Wachlevski, 2005
Thamnodynastes strigatus	Cycloramphidae	*Odontophrynus americanus*	Souza *et al*., 2003
Thamnodynastes strigatus	Ranidae	*Lithobates catesbeianus*	Souza *et al*., 2003
Thamnophis atratus	Ranidae	*Rana cascadae*	Garwood & Welsh Jr., 2005
Thamnophis cyrtopsis	Bufonidae	*Cranopsis occidentalis*	Abbadié-Bisogno *et al*., 2003
Thamnophis elegans	Ranidae	*Rana pretiosa*	Reaser & Dexter, 1996
Thamnophis hammindii	Bufonidae	*Anaxyrus californicus*	Griffin & Case, 2002
Thamnophis hammindii	Hylidae	*Pseudacris regilla*	Ervin & Fisher, 2001
Thamnophis hammindii	Pipidae	*Xenopus laevis*	Ervin & Fisher, 2001
Thamnophis hammindii	Scaphiopodidae	*Spea hammondii*	Ervin & Fisher, 2001
Thamnophis sauritus	Hylidae	*Osteopilus septentrionalis*	Love, 1995
Thamnophis scalaris	Ranidae	*Lithobates neovolcanica*	Romero *et al*., 2003
Thamnophis sirtalis	Leiopelmatidae	*Ascaphus truei*	Karraker, 2001
Thamnophis sirtalis	Hylidae	*Osteopilus septentrionalis*	Jansen, 1997
Thamnophis sirtalis	Ranidae	*Rana cascadae*	Garwood & Welsh Jr., 2005
Thamnophis sirtalis	Ranidae	*Rana muscosa*	Feldman & Wilkinson, 2000
Thamnophis sirtalis	Ranidae	*Rana aurora*	Maclay *et al*., 2004
Thamnophis valida	Scaphiopodidae	*Scaphiopus couchii*	Grismer, 2000
Xenochrophis flavopunctatus	Dicroglossidae	*Fejervaria limnocharis*	Pauwels, 2002
Xenoxybelis argenteus	Bufonidae	*Rhinella proboscidea*	Menin, 2005
Xenodon neuwiedii	Hylidae	*Bokermannohyla hylax*	Silva & Rodrigues, 2001

Hidrophiidae	*Pseudechis porphyriacus*	Bufonidae	*Chaunus marinus*	Fearn, 2003
Viperidae	*Agkistrodon piscivorus*	Ranidae	*Lithobates clamitans*	Cross, 2002
	Agkistrodon piscivorus	Ranidae	*Lithobates sphenocephala*	Cross, 2002
	Bothrops ammodytoides	Cycloramphidae	*Odontophrynus occidentalis*	Avila & Morando, 1998
	Bothrops asper	Brachycephalidae	*Eleutherodactylus* sp.	Greene, 1997
	Bothrops atrox	Leptodactylidae	*Leptodactylus fuscus*	Macedo-Bernarde & Bernarde, 2005
	Bothrops jararaca	Cycloramphidae	*Cycloramphus boraceiensis*	Giaretta & Nunes, 1997
	Porthidium nasutum	Brachycephalidae	*Eleutherodactylus* sp.	Greene, 1997
	Porthidium nasutum	Ranidae	*Lithobates warszewitschii*	Warner & Kolbe, 2003
Testudines				
Kinosternidae	*Kinosternon sonoriense*	Bufonidae	*Anaxyrus punctatus*	Ligon & Stone, 2003
Testudinidae	*Gopherus polyphemus*	Ranidae	*Lithobates sevosa*	Braid *et al*., 2000
Aves				
Accipitridae	*Haliaeetus leucocephalus*	Ranidae	*Lithobates catesbeianus*	Applegate, 1990
	Haliaeetus leucocephalus	Ranidae	*Lithobates palustris*	Applegate, 1990
Anatidae	*Buteo jamaicensis*	Bufonidae	*Anaxyrus boreas*	Jones & Stiles, 2000
	Buteo magnirostris	Leptodactylidae	*Leptodactylus ocellatus*	Souza *et al*., 2003
	Anas platyrhynchos	Ranidae	*Rana aurora*	Hayes & Rombough, 2004
	Anas platyrhynchos	Ranidae	*Rana boylii*	Bombough *et al.*, 2005
	Anas platyrhynchos	Ranidae	*Rana temporaria*	Bombough *et al.*, 2005
	Anas platyrhynchos	Ranidae	*Lithobates sylvaticus*	Bombough *et al.*, 2005
	Oxyura ferruginea	Ceratophryidae	*Atelognathus patagonicus*	Cuello *et al.*, 2005
Ardeidae	*Ardea herodias*	Pipidae	*Xenopus laevis*	Crayon & Hothem, 1998
	Ardea herodias	Ranidae	*Rana aurora*	Fellers & Wood, 2004
	Nycticorax nycticorax	Pipidae	*Xenopus laevis*	Crayon & Hothem, 1998
	Tigrisoma lineatum	Hylidae	*Pseudis paradoxa*	Prado, 2003
	Tigrisoma lineatum	Leptodactylidae	*Leptodactylus chaquensis*	Prado, 2003
Corvidae	*Corvus macrorhynchos*	Bufonidae	*Bufo parietalis*	Krishna & Vijayalaxmi, 2004
Cracidae	*Penelope superciliaris*	Brachycephalidae	*Brachycephalus ephippium*	Carvalho, 1941
Cuculidae	*Guira guira*	Leptodactylidae	*Physalaemus* cf. *fuscomaculatus*	Kokubum & Zacca, 2003
	Piaya cayana	Hylidae	*Osteocephalus taurinus*	Cintra & Sanaiotti, 1990
Falconidae	*Polyborus plancus*	Hylidae	*Bokermannohyla alvarengai*	Machado & Galdino, 2005
Icteridae	*Quiscalus quiscula*	Scaphiopodidae	*Scaphiopus holbrookii*	Palis, 2000
Laridae	*Larus delawarensis*	Bufonidae	*Anaxyrus fowleri*	Smith & Green, 2005

	Larus maculipennis	Ceratophryidae	*Atelognathus patagonicus*	Cuello *et al.*, 2005
Momotidae	*Baryphthengus martii*	Dendrobatidae	*Dendrobates auratus*	Master, 1998
Odontophoridae	*Colinus virginianus*	Scaphiopodidae	*Scaphiopus hurterii*	McCoid *et al*., 1999
Phalacrocoracidae	*Phalacrocorax carbo*	Pipidae	*Xenopus laevis*	Kopij, 1998
	Phalacrocorax carbo	Pyxicephalidae	*Amietia angolensis*	Kopij, 1998
Podicipedidae	*Podiceps occipitalis*	Ceratophryidae	*Atelognathus patagonicus*	Cuello *et al.*, 2005
	Podiceps rolland	Ceratophryidae	*Atelognathus patagonicus*	Cuello *et al.*, 2005
Sturnidae	*Sturnus vulgaris*	Scaphiopodidae	*Scaphiopus holbrookii*	Palis, 2000
Threskiornithidae	*Theristicus caudatus*	Bufonidae	*Chaunus granulosus*	Carvalho, 1941
	Theristicus caudatus	Microhylidae	*Elachistocleis* cf. ovalis	Carvalho, 1941
Tinamidae	*Tinamus solitarius*	Brachycephalidae	*Brachycephalus ephippium*	Carvalho, 1941
Trogonidae	*Trogon surrucura*	Hylidae	*Hypisboas albomarginatus*	Toledo *et al*., 2005
	Trogon surrucura	Hylidae	*Hypsiboas bischoffi*	Toledo *et al*., 2005
	Trogon surrucura	Hylidae	*Phyllomedusa distincta*	Toledo *et al*., 2005
Tyranidae	*Pitangus sulphuratus*	Hylidae	*Scinax nasicus*	Toledo *et al*., 2005; Ávila, 2005
Tytonidae	*Tyto alba*	Leptodactylidae	*Eupemphix nattereri*	C. F. B. Haddad, unpubl. data
	Tyto alba	Ranidae	*Lithobates sphenocephalus*	Briggler, 2000
Mammalia				
Carnivora				
Canidae	*Cerdocyon thous*	Leptodactylidae	*Eupemphix nattereri*	Bezerra, 1998
	Chrysocyon brachyurus	Bufonidae	*Chaunus ictericus*	Guix, 1993
	Chrysocyon brachyurus	Leptodactylidae	*Leptodactylus labyrinthicus*	Prado *et al*., 2005
	Vulpes vulpes	Bufonidae	*Anaxyrus boreas*	Jones *et al*., 1999
Mustelidae	*Galictis vittata*	Bufonidae	*Chaunus marinus*	Cintra, 1988
	Lontra canadensis	Ranidae	*Rana pretiosa*	Hayes *et al.*, 2005
	Lutra longicaudis	Leptodactylidae	*Leptodactylus pentadactylus*	Roberts, 1997A
	Lutra longicaudis	Ranidae	*Rana pretiosa*	Roberts, 1997B
	Mustela putorius	Bufonidae	*Bufo bufo*	Lodé, 1996
	Mustela putorius	Ranidae	*Rana dalmatina*	Lodé, 1996
	Mustela putorius	Ranidae	*Pelophylax esculentus*	Lodé, 1996
	Mustela vison	Ranidae	*Lithobates palustris*	Beane, 1990
Procyonidae	*Procyon lotor*	Bufonidae	*Anaxyrus boreas*	Jones *et al*., 1999
	Procyon cancrivorus	Bufonidae	*Chaunus ictericus*	Guix, 1993

Chiroptera				
Phyllostomatidae	*Trachops cirrhosus*	Leptodactylidae	*Engystomops pustulosus*	Tuttle *et al*., 1982
Insetivora				
Erinaceidae	*Atelerix pruneri*	Bufonidae	*Bufo alvarius*	Brodie Jr., 1977
	Atelerix pruneri	Bufonidae	*Anaxyrus americanus*	Brodie Jr., 1977
	Atelerix pruneri	Bufonidae	*Anaxyrus boreas*	Brodie Jr., 1977
	Atelerix pruneri	Bufonidae	*Chaunus marinus*	Brodie Jr., 1977
	Atelerix pruneri	Bufonidae	*Anaxyrus quercicus*	Brodie Jr., 1977
	Atelerix pruneri	Bufonidae	*Amietophrynus regularis*	Brodie Jr., 1977
	Atelerix pruneri	Bufonidae	*Anaxyrus terrestris*	Brodie Jr., 1977
	Atelerix pruneri	Bufonidae	*Anaxyrus woodhousii*	Brodie Jr., 1977
	Atelerix pruneri	Ranidae	*Lithobates catesbeianus*	Brodie Jr., 1977
	Hemiechinus auritus	Bufonidae	*Bufo alvarius*	Brodie Jr., 1977
	Hemiechinus auritus	Bufonidae	*Anaxyrus americanus*	Brodie Jr., 1977
	Hemiechinus auritus	Bufonidae	*Anaxyrus boreas*	Brodie Jr., 1977
	Hemiechinus auritus	Bufonidae	*Chaunus marinus*	Brodie Jr., 1977
	Hemiechinus auritus	Bufonidae	*Anaxyrus quercicus*	Brodie Jr., 1977
	Hemiechinus auritus	Bufonidae	*Amietophrynus regularis*	Brodie Jr., 1977
	Hemiechinus auritus	Bufonidae	*Anaxyrus terrestris*	Brodie Jr., 1977
	Hemiechinus auritus	Bufonidae	*Anaxyrus woodhousii*	Brodie Jr., 1977
	Hemiechinus auritus	Ranidae	*Lithobates catesbeianus*	Brodie Jr., 1977
Soricidae	*Blarina brevicauda*	Hylidae	*Hyla versicolor*	Brodie Jr. & Formanowicz Jr., 1981
Marsupialia				
Didelphidae	*Didelphis marsupialis*	Bufonidae	*Chaunus marinus*	Garrett & Boyer, 1993
	Philander opossum	Hylidae	*Hypsiboas rosenbergi*	Kluge, 1981
Primates				
Callitrichidae	*Callithrix penicillata*	Hylidae	*Hypsiboas lundii*	Canale & Lingnau, 2003
Rodentia				
Muridae	*Rattus rattus*	Leiopelmatidae	*Leiopelma archeyi*	Thurley & Bell, 1994

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