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Predation of Juvenile and Adult Anurans by Invertebrates: Current Knowledge and Perspectives

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Anuran amphibians are preyed on by vertebrates, invertebrates, and even carnivorous plants (Duellman and Trueb 1994). Most of these reports on predation are anecdotal (Fitch 1987; Greene 1993) and do not provide data other than a short description of the predatory event (e.g., Boistel and Pauwels 2002; Brandão and Garda 2000; Del-Grande and Moura 1997; Mitchell 1990). The scattered information on the subject makes it difficult to identify patterns. Additionally, McCormick and Polis (1982) pointed out the lack of quantitative data evaluating the impact of arthropod predators upon vertebrates. This is particularly true for predation by invertebrates upon post-metamorphic (generally adult) anurans. For example, reports on this subject usually state that few cases of invertebrate predation upon anurans are recorded (e.g., Bastos et al. 1994; Bernarde et al. 1999; Del-Grande and Moura 1997; Hinshaw and Sullivan 1990; Mitchell 1990), when, in fact, a considerable amount of information is generally available (e.g., McCormick and Polis 1982). Therefore, I review the subject in an attempt to depict our current knowledge, add unpublished data, and provide a background to which new reports may be added.

By reviewing published information on the subject I collected data on a wide range of taxa, i.e., at least 68 post-metamorphic (juvenile to adult) anuran species preyed upon by at least 57 invertebrate species, including arachnids, crabs, leeches, and various insect groups (Tables 1 and 2). Besides the species listed (Table 2), there exists indirect evidence and laboratory studies that add

Table 1. Invertebrate predators and number of species reported to prey upon post-metamorphic anuran amphibians.

Class	Order	Family	Common name	Abbreviation	Number Of species
Hirudinea	Arhynchobdellida	Hirudinidae	Leeches	Ah	1
Chilopoda	Scolopendromorpha	Scolopendridae	Giant centipedes	Gc	1
Arachnida	Scorpiones	Buthidae	Scorpions	Sc	1
	Uropygi	Thelyphonidae	Vinegaroons	Ut	1
	Amblypygi	Ambypigidae	Amblypigids	Am	1
	Araneae	Araneidae	Orb weavers	Aa	3
		Ctenidae	Wandering spiders	Ac	2
		Ctenizidae	Trapdoor spiders	Az	1
		Dipluridae	Tarantulas	Ad	1
		Lycosidae	Wolf spiders	Al	6
		Pisauridae	Fishing spiders	Ap	10
		Sparassidae	Crab spiders	As	1
		Theraphosidae	Tarantulas	At	6
Malacostraca	Decapoda	Coenobitidae	Crabs	Dc	1
Hexapoda	Coleoptera	Carabidae	Ground beetles	Cb	3
		Cicindelidae	Tiger beetles	Cc	1
		Dytiscidae	Diving beetles	Cd	1
	Diptera	Tabanidae	Horse flies	Di	1
	Hemiptera	Belostomatidae	Water bugs	Hb	8
		Nepidae	Water scorpions	Hn	1
	Hymenoptera	Formicidae	Ants	Hf	4
	Mantodea	Mantidae	Preying mantis	Mm	1
	Neuroptera	Corydalidae	Hellgrammites	Ch	1

other potential invertebrate predators to the list, such as spiders (*Oilos antaguensis*, *Stasina portoricensis*, and *Avicularia latea*), amblypygids (*Phrynus longipes*), and forest crabs (*Epilobocera situatifrons*) (Formanowicz et al. 1981; Stewart 1995). Laboratory studies using pipid and hyperoliid frogs report pisaurid spiders as additional potential predators upon previously unreported anuran families (Table 2).

It appears that many anuran species can be preyed upon by invertebrate predators, independent of prey body size/age (see discussion in McCormick and Polis 1982), phylogeny, or recognized presence of an elevated quantity of biologically active skin secretions (Duellman and Trueb 1994) (Table 2). However, the risk of predation by invertebrates seems to be greater in two crucial periods of the anurans life cycle: 1) during the breeding season, when most species enter the water and consequently are in contact with potential aquatic predators (e.g., Bastos et al. 1994; Haddad and Bastos 1997; Toledo 2003); and 2) when the recently-metamorphosed frogs are about to leave or actually leave the water (Fig. 1), thus facing both aquatic and terrestrial invertebrates (e.g., Clerke and Williamson 1992; Hirai and Hidaka 2002; Robertson 1989; Toledo 2003). Almost 90% of the observations that provide descriptions of the frog behavior before the predation were recorded during these two stages.

Predation events occurred both in and out of the water and about 73% of them involved water bugs (approximately 25%) and spiders (approximately 48%) as anuran predators (Fig. 2). This may reflect the high density of these animals in nature (DuBois and Gobin 2001; Formanowicz et al. 1981; McCormick and Polis 1982; and references therein). Additionally, it could indicate that spiders and water bugs may be significant predators of anuran populations (Formanowicz et al. 1981; Toledo 2003), though, few studies have determined actual predation rates on adult anurans (e.g., Haddad and Bastos 1997; Hinshaw and Sullivan 1990).

In reviewing the subject I was able to identify a few cases of incorrect or repeated data. For example, Nauman and Dettlaff (1999) reported "the first published record of a giant water bug preying on an adult frog"; however, at least three reports on giant water bugs preying on adult frogs were already available by that time (Bastos et al. 1994; Haddad and Bastos 1997; Hinshaw and Sullivan 1990). Additionally, both Toledo (2003) and Brasileiro

Fig. 1. Juvenile *Hyla albosignata* being preyed upon by a tarantula on vegetation near a stream in a forested area, Municipality of Pilar do Sul, State of São Paulo, Brazil. Photograph by André Antunes.

TABLE 2. Post-metamorphic (juvenile to adult) anurans (15 families; at least 68 species) reported as prey of invertebrates (22 families; at least 57 species) and the microhabitat where the predation occurred. Anuran specific names follow Frost (2004), and thus some genera and species are updated. Predators' abbreviations are in table 1. An asterisk (*) after the anuran names indicates the recognized presence of a high amount of biologically active skin secretions.

Anurans (Prey)	Invertebrates (Predators)	Predation microhabitat	References
Ascaphidae			
Ascaphus truei	Hellgrammite – unidentified (Mh)	Pool in the stream	Jones and Raphael, 1998
Bufonidae			
Bufo bufo *	*Formica rufa* (Hf)	Lake margin	Zuffi, 2001
Bufo crucifer *	*Lethocerus grandis* (Hb)	Temporary pond	Haddad and Bastos, 1997
Bufo houstonensis *	*Solenopsis invicta* (Hf)	Litter	Thomas and Allen, 1997
Bufo marinus *	*Iridomyrmex purpureus* (Hf)	Pond margin	Clerke and Williamson, 1992
Bufo marinus *	*Scolopendra alternans* (Gc)	Leaf litter	Carpenter and Gillingham, 1984
Bufo terrestris *	*Lethocerus* sp. (Hb)	Temporary pond	McCoy, 2003
Centrolenidae			
Centrolene prosoblepon	*Cupiennus* sp. (Ac)	Over rocks, near the water	Hayes, 1983
Hyalinobatrachium fleischmanni	*Cupiennus* sp. (Ac)	Over leaf	Hayes, 1983
Dendrobatidae			
Colostethus inguinalis	Freshwater crab – unidentified (Dc)	Not provided	Duellman and Trueb, 1994
Dendrobates auratus *	*Sericopelma rubronitens* (At)	Litter	Summers, 1999
Dendrobates pumilio *	*Paraponera clavata* (Hf)	Litter	Fritz et al., 1981
Hylidae			
Acris crepitans	*Hogna helluo* (Al)	Semi-permanent wetland	Blackburn et al., 2002
Acris gryllus	*Dolomedes* sp. (Ap)	Edges of water body	Goin, 1943
Hyla albomarginata	*Belostoma* sp. (Hb)	Temporary pond	Froehlich, 2001
Hyla albosignata	Tarantula – unidentified (At)	Vegetation over water	A. Antunes, unpubl. data
Hyla cinerea	*Dolomedes okefinokensis* (Ap)	Vegetation over water	Jeffery et al., 2004
Hyla cinerea	*Acanthepeira stellata* (Aa)	Not provided	Lockley, 1990
Hyla crepitans	*Belostoma* sp. (Hb)	Permanent pool	Mijares-Urrita et al., 1997
Hyla ebraccata	*Cupiennius coccineus* (Ac)	Swamp	Szelistowski, 1985
Hyla japonica	*Diplonychus japonicus* (Hb)	Flooded rice field	T. Hirai, unpubl. data
Hyla japonica	*Dolomedes sulfurous* (Ap)	Flooded rice field	T. Hirai, unpubl. data
Hyla japonica	*Laccotrephes japonensis* (Hn)	Flooded rice field	T. Hirai, unpubl. data
Hyla japonica	*Lethocerus deyrollei* (Hb)	Flooded rice field	Hirai and Hidaka, 2002
Hyla jimi	*Belostoma elongatum* (Hb)	Temporary pond	Toledo, 2003
Hyla minuta	*Belostoma elongatum* (Hb)	Temporary pond	Toledo, 2003
Hyla minuta	*Lethocerus delpontei* (Hb)	Permanent pond	Bastos et al., 1994
Hyla minuta	*Dolomedes* sp. (Ap)	Permanent pond	Bastos et al., 1994
Hyla minuta	*Ancylometes vulpes* (Ap)	Permanent pond	Bernarde et al., 1999
Hyla minuta	*Ancylometes gigas* (Ap)	Permanent pond	Bernarde et al., 1999
Hyla miotympanum	*Abedus* sp. (Hb)	Permanent stream	Pineda, 2003
Hyla nana	*Thaumasia* sp. (Ap)	Swamp	Pramuk and Alamillo, 2002
Hyla sanborni	*Diapontia cf. uruguayensis* (Al)	Web over pond	Del-Grande and Moura, 1997
Hyla versicolor	*Argiope aurantia* (Aa)	Web near pond	Steehouder, 1992
Hyla versicolor	*Lethocerus americanus* (Hb)	Pond	Hinshaw and Sullivan, 1990
Litoria caerulea	*Hierodula werneri* (Mm)	Not provided	Ridpath, 1977
Litoria caerulea	*Atrax formidobilis* (Ad)	Not provided	McCormick and Polis, 1982
Litoria ewingi	*Catadromus lacordairei* (Cb)	Not provided	LittleJohn and Wainer, 1978
Litoria lesueurii	*Lycosa lapidosa* (Al)	On the rocks of a creek bed	Raven, 1990
Litoria raniformis	*Archimantis latistyla* (Mm)	Not provided	Ridpath, 1977
Pseudacris crucifer	Diving beetle – unidentified (Cd)	Temporary pond	Hinshaw and Sullivan, 1990
Pseudacris feriarum	*Dolomedes triton* (Ap)	Temporary pond	Mitchell, 1990
Pseudacris ocularis	*Lycosa* sp. (Al)	Ground, near water body	Owen and Johnson, 1997
Scinax alter	*Ancylometes rufus* (Ap)	Over aquatic vegetation	Prado and Borgo, 2003
Scinax alter	*Thaumasia* sp. (Ap)	Water surface	Marra et al., 2003
Scinax cruentommus	Wolf spider – unidentified (Al)	Vegetation over ground	Aucone and Card, 2002
Scinax elaeochroa	*Cupiennius coccineus* (Ac)	Swamp	Szelistowski, 1985
Scinax fuscomarginatus	*Oxyuptychus brasiliensis* (Ah)	Vegetation over pond	Brand„o and Garda, 2000
Scinax fuscomarginatus	Tarantula – unidentified (At)	Temporary pond	L. F. Toledo, unpubl. data
Scinax fuscomarginatus	Water bug – unidentified (Hb)	Temporary pond	L. F. Toledo, unpubl. data
Scinax ruber	Preying mantis – unidentified (Mm)	Over vegetation	J. L. Guillaumet, unpubl. data
Scinax squalirostris	*Belostoma elongatum* (Hb)	Temporary pond	Toledo, 2003

TABLE 2. Continued.

Anurans (Prey)	Invertebrates (Predators)	Predation microhabitat	References
Scinax sp. (*aff. similis*)	*Belostoma elongatum* (Hb)	Temporary pond	Toledo, 2003
Hyperoliidae			
Hyperolius marmoratus	*Thalassius fimbriatus* (Ap)	Laboratory situation	McCormick and Polis, 1982
Leptodactylidae			
Eleutherodactylus coqui	*Olios* sp. (As)	Above ground	Formanowicz Jr. et al., 1981
Eleutherodactylus coqui	*Oligoctenus ottleyi* (Al)	Not provided	Formanowicz Jr. et al., 1981
Eleutherodactylus coqui	*Phrynus palmatus* (Am)	Not provided	Formanowicz Jr. et al., 1981
Eleutherodactylus coqui	*Tityus obtusus* (Sc)	Vegetation over ground	Villanueva-Rivera et al., 2000
Eleutherodactylus zugi	*Ctenus vernalis* (Ac)	Ground inside cave	Novo et al., 1985
Eleutherodactylus sp.	*Paraponera clavata* (Hf)	Litter	Fritz et al., 1981
Eleutherodactylus spp.	*Cupiennius coccineus* (Ac)	Experimental condition	Szelistowski, 1985
Hylodes phyllodes	*Trachalea keyserlingi* (Ap)	Leaf litter next to a stream	Schiesari et al., 1995
Leptodactylus knudseni *	*Theraphosa lebondi* (At)	Not provided	Boistel and Pauwels, 2002
Leptodactylus labyrinthicus *	*Belostoma elongatum* (Hb)	Temporary pond	Toledo, 2003
Leptodactylus ocellatus	*Lethocerus annulipes* (Hb)	Not provided	Lima, 1940
Physalaemus cuvieri	*Belostoma elongatum* (Hb)	Temporary pond	Toledo, 2003, Brasileiro et al., 2003
Physalaemus fuscomaculatus *	*Belostoma elongatum* (Hb)	Temporary pond	Toledo, 2003
Physalaemus cf. fuscomaculatus *	*Lethocerus* sp. (Hb)	Temporary pond	Giaretta and Menin, 2004
Physalaemus pustulosus	*Sericopelma rubronitens* (At)	Leaf litter	Gray et al., 1999
Physalaemus spiniger	Wolf spider – unidentified (Al)	Temporary pond	L. M. Giasson, unpubl. data
Limnodynastidae			
Limnodynastes tasmaniensis	*Catadromus lacordairei* (Cb)	Not provided	LittleJohn and Wainer, 1978
Neobatrachus centralis	*Selenotypus* sp. (At)	Not provided	Raven, 1990
Neobatrachus centralis	*Selenocosmia crassipes* (At)	Not provided	McCormick and Polis, 1982
Microhylidae			
Microhyla ornata	*Lycosa carmichaeli* (Al)	Not provided	McCormick and Polis, 1982
Myobatrachidae			
Crinia pseudinsignifera	*Aganippe raphiduca* (Az)	Ground, near spider burrow	Butler and Main, 1959
Crinia signifera	*Chlaenius darlingensis* (Cb)	Margin of pond	Robertson, 1989
Uperoleia laevigata	*Chlaenius darlingensis* (Cb)	Margin of pond	Robertson, 1989
Pelobatidae			
Spea multiplicata	*Tabanus punctifer* (Di)	Mud margin of pond	Jackman et al., 1983
Spea multiplicata	*Cicindela sedecimpunctata* (Cc)	Not provided	McCormick and Polis, 1982
Pipidae			
Xenopus laevis *	*Dolomedes triton* (Ap)	Laboratory situation	Rogers, 1996
Rhacophoridae			
Rhacophorus arboreus	*Cybister japonicus* (Cd)	Flooded rice field	T. Hirai, unpubl. data
Rhacophorus schlegelii	*Laccotrephes japonensis* (Hn)	Flooded rice field	T. Hirai, unpubl. data
Rhacophorus schlegelii	*Lethocerus deyrollei* (Hb)	Flooded rice field	Hirai and Hidaka, 2002
Ranidae			
Euphlyctis cf. cyanophlyctis	*Lycosa barmanica* (Al)	Not provided	McCormick and Polis, 1982
Fejervarya limnocharis	*Lethocerus deyrollei* (Hb)	Flooded rice field	Hirai and Hidaka, 2002
Rana cascadae	*Lethocerus* sp. (Hb)	Lake	Nauman and Dettlaff, 1999
Rana clamitans	Wolf Spider – unidentified (Al)	Grass field	Neil, 1948
Rana nigromaculata	*Epomis nigricans* (Cb)	Flooded rice field	T. Hirai, unpubl. data
Rana nigromaculata	*Lethocerus deyrollei* (Hb)	Flooded rice field	Hirai and Hidaka, 2002
Rana porosa	*Lethocerus deyrollei* (Hb)	Irrigation ditch (rice field)	T. Hirai, unpubl. data
Rana rugosa	*Lethocerus deyrollei* (Hb)	Flooded rice field	T. Hirai, unpubl. data
Unidentified anurans			
Frog	*Grammostola* sp. (At)	Not provided	McCormick and Polis, 1982
Frog	*Lasidora* sp. (At)	Not provided	McCormick and Polis, 1982
Frog	*Birgus latro* (Dc)	Not provided	McCormick and Polis, 1982
Frogs and toads	*Mastigoproctus giganteus* (Ut)	Not provided	McCormick and Polis, 1982
Green Frog	*Nephila plumipes* (Aa)	Not provided	McCormick and Polis, 1982
Green Tree Frog	*Nephila plumipes* (Aa)	Not provided	McCormick and Polis, 1982
Leptodactylidae, Brown Frogs	Wolf Spider – unidentified (Al)	Not provided	McCormick and Polis, 1982
Tree Frog	*Dolomedes okefenokensis* (Ap)	Not provided	McCormick and Polis, 1982

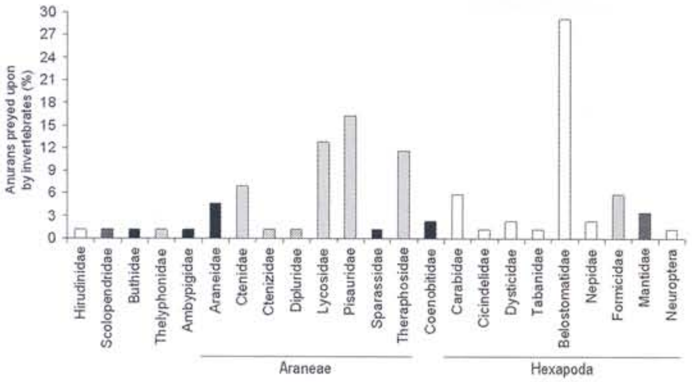

FIG. 2. Percentage of different anuran species that were preyed upon by different invertebrate families based on references listed in Table 2 (N_{total} = 89 accounts). White bars indicate predation events reported to occur in the water; dark bars indicate predation events out of the water; gray bars indicate predation events both in and out of the water; and striped bars represent lack of information on the microhabitat in which the predation occurred.

et al. (2003) provided duplicate reports of the predation of *Physalaemus cuvieri* by the same water bug species (*Belostoma elongatum*) at the same study site. Nevertheless, repeated records may be beneficial as they provide more evidence for an actual predator-prey relationship, and may help determine if any geographic variation occurs in the predator-prey relationship.

Despite the considerable number of reports much more information is likely to appear in the next few years. However, the simple descriptions of a predatory event without providing further details (e.g., microhabitat and prey activity before predation - data that should generally be available to the observers) make future discussions and predictions difficult (see Greene 1993). Therefore, even reports on simple interactions between predator and prey (particularly in the context discussed here) should provide more detailed accounts whenever possible (see complementary discussions in Greene 1986; 1993).

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TECHNIQUES

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Application and Evaluation of a Stomach Flushing Technique for Alligators

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Crocodilian diets can be studied by observing what an animal eats, conducting feeding trials on captive animals, performing biochemical and isotope analysis, or by obtaining samples of the ingested food from the stomachs of wild animals. Stomach contents can be obtained post-mortem from specimens killed for that purpose or collected incidentally from commercial harvests. However, many crocodilian species are threatened or endangered and there are ethical and practical constraints on killing animals for study. Therefore, non-lethal methods have been developed to obtain stomach contents from live crocodilians without causing them harm.

Non-lethal methods used to obtain the stomach contents of crocodilians fall into three categories: invasive scoops that mechanically retrieve material through the esophagus (Taylor et al. 1978), irrigation methods that introduce water and flush material from the stomach (Fitzgerald 1989; Taylor et al. 1978) and combinations of these (Webb et al. 1982). These methods vary in effectiveness at recovering all the stomach contents, ease of application in the field and degree of invasive trauma to the animal. The purpose of this study is to evaluate the hose-Heimlich technique (irrigation method) for accuracy and to check for internal damage on American Alligators (*Alligator mississippiensis*). We also report on the effectiveness of the hose-Heimlich technique used during an alligator diet study, and we investigate alternative water sources for use with this technique.

The hose-Heimlich technique described by Fitzgerald (1989) was used to obtain the stomach contents from live adult American