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On the Diet of the Frogs of the Ceratophryidae: Synopsis and New Contributions

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Abstract. The frogs of the family Ceratophryidae (comprised of three genera containing 12 species) are well known for their voracious feeding behavior and unique morphologies in both larval and post-metamorphic life stages. Nevertheless, relatively little is known about the diet of these species, especially in nature. We summarized the current knowledge of the diet of larval and post-metamorphic ceratophryids in both natural and experimental settings by conducting a literature review, specimen dissections, and field observations. Prior to this study, diet information did not exist for one fourth of the species in the family: *Ceratophrys calcarata, Ceratophrys joazeirensis Ceratophrys stolzmanni,* and *Ceratophrys testudo.* We add, for the first time, information on the diet of *Ceratophrys calcarata.* In addition, our survey revealed that relatively few detailed studies with large sample sizes have been conducted on the diet of these frogs. Frequently, knowledge of the diet of a species is derived from palatability experiments using captive individuals (often a single individual). From those diet studies that were conducted under natural conditions, ceratophryids can be classified as generalist, opportunistic predators, often preying on a wide variety of invertebrate and vertebrate prey. All species of ceratophryids for which we obtained information on diet were found to consume vertebrates, with anuran prey occurring in nearly all species. Even less is known about the diet of the tadpoles of these species; while cannibalism is assumed to be widespread, we found evidence for cannibalism at the larval stage in only three species. Future studies should attempt to understand the trophic ecology of these species under natural scenarios at both life stages, and an ontogenetic approach using individuals across multiple size classes could elucidate the niche shifts associated with these species from larva to adult.

Keywords. Anurans; Cannibalism; *Ceratophrys; Chacophrys;* Feeding behavior; *Lepidobatrachus;* Prey; Tadpole.

INTRODUCTION

> "They [Intanha; *Ceratophrys aurita*] are fearless and react to any attack, running with their mouths open behind their aggressors. ... They can grab everything that is in their reach and that moves; they do not neglect even chicks as big and voluminous as they are."
>
> (Miranda-Ribeiro, 1920; translated by H.R. da Silva).

Frogs of the family Ceratophryidae have long fascinated biologists, which has resulted in a body of literature that predates Linnaeus and rivals in size that for other similarly sized groups of frogs (e.g., Seba, 1734; Linnaeus, 1758; Shaw, 1802). Ceratophryidae is comprised of three genera; *Ceratophrys* is the most species-rich genus with eight species, followed by *Lepidobatrachus* (three species), and the monotypic genus containing *Chacophrys pierottii* (Frost, 2014). *Ceratophrys* is distributed throughout tropical South America, ranging from the Caribbean lowlands of Venezuela and Colombia in the north, and the Pacific coast of Ecuador in the west, southward through Amazonia to the Gran Chaco of central Argentina and eastward into the Cerrado of southeastern Brazil (Lynch, 1982; Frost, 2014). All three species of *Lepidobatrachus* and *C. pierottii,* on the other hand, are endemic to the Gran Chaco ecoregion of central South America (Cei, 1980).

As adults, species of *Ceratophrys* and *Chacophrys pierottii* are more terrestrial than those of *Lepidobatrachus,* which are aquatic and inhabit temporary pools during the rainy season in the Gran Chaco (Cei, 1955, 1958, 1968, 1980). All species of ceratophryids, however, are considered sit-and-wait ambush predators (Duellman and Lizana, 1994; Scott and Aquino, 2005) and their behaviors and morphologies that reflect such a foraging mode have become legendary. All species of ceratophryids, for example, possess a wide gape and fang-like teeth, which are presumed to be traits adapted for consuming large, slow-moving prey such as vertebrates (e.g., Emerson, 1985; Fabrezi and Emerson, 2003; Fig. 1).

The tadpoles of ceratophryids are equally as remarkable as the adults. Those of species of *Ceratophrys* and *Lepidobatrachus* possess morphologies indicative of their macrophagous and carnivorous habits (Cei, 1968; Rubial and Thomas, 1988; Altig and McDiarmid, 1999; Wild, 1997a, 1997b; Natale et al., 2011; Wassersug and Heyer, 1988). Tadpoles of the species of *Lepidobatrachus* have some of the most distinctive body morphologies of any anuran larvae, with their wide, dorsoventrally flattened head and lack of keratinized mouthparts, which allow them to engulf prey whole (Cei, 1968; Rubial and Thomas,

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1988). The mouths of tadpoles of the species of *Ceratophrys,* on the other hand, are terminal and contain strong, keratinized jaw sheaths and keratodonts that facilitate biting and chewing of prey (Wild, 1997a, 1997b; Altig and McDiarmid, 1999; Vera Candioti, 2005). The tadpole of *Chacophrys pierottii,* however, lacks such distinctive traits and has a body plan and morphology similar to that of a Type IV tadpole (Orton, 1953; Wild, 1999; Quinzio et al., 2006) and is considered a member of the benthic ecomorphological guild (Altig and McDiarmid, 1999).

The literature is replete with comments regarding the carnivorous ambitions of ceratophryid frogs, including cannibalism, at all stages in their life cycle (e.g., Noble, 1931, Parker, 1931; Cei, 1980). However, with a few exceptions (e.g., Basso, 1990; Duellman and Lizana, 1994; Pueta and Perotti, 2013), there is little published data on the diet of most species of the Ceratophryidae, and that which exists is scattered among anecdotal reports (e.g., feeding observations of a single captive tadpole; Miranda-Ribeiro, 1923) or is overly general (e.g., "…feeding on small vertebrates and arthropods…", Cei, 1980). Herein we provide a comprehensive synopsis of the current state of knowledge of the diet of these remarkable frogs throughout their life cycle stages from results of a comprehensive survey of the literature, from field observations, and from specimen-based research.

Figure 1. (A) An adult *Ceratophrys cornuta* consuming a medium-sized (ca. 50–90 g) oryzomyine rodent (e.g., *Euryoryzomys* or *Hylaeamys*) at Reserva Amazonica on the Río Madres de Dios, Departamento de Madre de Dios, Peru (photo by Kyle Salzmann). **(B)** An adult female *Ceratophrys cranwelli* consuming a *Rhinella major* (Anura: Bufonidae) in a temporary pond in the community of Yaprioa, Provincia Cordillera, Departamento de Santa Cruz, Bolivia (photo by C.M. Schalk).

MATERIALS AND METHODS

Literature review

We surveyed the literature to provide a comprehensive list of known prey items of the species within Ceratophryidae. We used Web of Knowledge and Google Scholar to search for published articles, books, and book chapters using the following keywords: "Ceratophryidae", "*Ceratophrys*", "*Chacophrys*", "*Lepidobatrachus*", "prey", "diet", "food", and "tadpole". Additional references were gathered from searching through the literature cited sections of the sources produced from our database searches. Our search included both tadpole and post-metamorphic life stages, under both natural (e.g., field observations or specimen dissections) and captive (e.g., feeding experiments) conditions but only with native prey. Thus, experiments conducted with non-native prey or reports of captive feeding on non-native prey, although intriguing (e.g., a specimen of *Ceratophrys* eating an 11 inch *Alligator mississippiensis;* Parsons, 1932), were not included in our survey as they address what these frogs *can* eat. We are interested in what they *do* eat in nature.

Specimen dissections

We dissected 21 individuals from seven species of ceratophryids (Appendix): *Ceratophrys aurita* (*n* = 3), *Ceratophrys calcarata* (*n* = 2), *Ceratophrys cranwelli* (*n* = 2), *Ceratophrys ornata* (*n* = 2), *Chacophrys pierottii* (*n* = 9), *Lepidobatrachus asper* (*n* = 2), *Lepidobatrachus laevis* (*n* = 1). We counted and identified items in the stomach and intestine to the lowest taxonomic level possible. We grouped food items into generalized categories and calculated the percent frequency of occurrence for each species. Because most of the prey items were incomplete, and we lacked a reference collection for sizes of prey items, we did not calculate their percent volume in the gut of the specimens.

Field observations

We report five new prey items for ceratophryid frogs through direct observations in the field. Three new prey items are documented for larval and post-metamorphic

Ceratophrys cranwelli gathered from opportunistic encounters by one of us (CMS) in the dry Chaco forest of southeast Bolivia around the community of Yapiroa, Provincia Cordillera, Departmento de Santa Cruz, Bolivia (19°36'15"S, 62°34'32"W). The dry Chaco is a xerophytic thorn forest with a distinct rainy (November–March) and dry (October–November) season, averaging 513 mm of rainfall annually in this region (Navarro and Maldonado, 2002). Another new prey item is documented from an opportunistic encounter (ERW) in the diet of adult *Ceratophrys cornuta* from Reserva Amazonica, Peru. Reserva Amazonica is a tourist lodge and reserve on the north bank of the Río Madre de Dios, about 15 km ENE of Puerto Maldonado, Provincia de Tambopata, Departamento de Río Madre de Dios, Peru (12°33'S, 69°03'W; 200 m) (Duellman and Koechlin, 1991). The climate is seasonally tropical with distinct rainy (October–March) and dry (May–July) seasons and an average annual rainfall of 2416 mm. The region is mapped as a humid tropical forest, but is situated near the transition between humid tropical forest and dry tropical forest (Tosi, 1960). Another new prey item is documented in the diet of *Lepidobatrachus laevis* from field observations at Laguna Yema Formosa, Argentina (J. Faivovich pers. comm.).

RESULTS

Our literature survey found 42 references on the diet of eight of the twelve species of Ceratophryidae from captive and field studies (Tables 1 and 2, respectively); this total does not include citations of previous reports. Those species for which no data could be found in the literature are *Ceratophrys calcarata, C. joazeirensis, C. stolzmanni,* and *C. testudo.* Six of these eight ceratophryid species had information on tadpole diet, with sample sizes ranging from one to seven individuals. We provide novel observations regarding tadpole diet for only *C. cranwelli.* Regarding post-metamorphic diet we found literature information for all eight of these species, with sample sizes (again when reported) ranging from one to seventy-two individuals. Our field observations and stomach content analyses provide additional post-metamorphic diet information (sample sizes ranging from one to nine) for all eight of these species except *Lepidobatrachus llanensis,* but with the addition of *C. calcarata.* Herein we provide a compilation of all these data, from both the literature and our observations (field and stomach content analysis), in the form of species accounts in which we first address tadpole diet, and then the diet of post-metamorphic life stage.

Ceratophrys aurita

In captivity, the tadpoles of *Ceratophrys aurita* have been observed consuming three species of tadpoles, (Miranda-Ribeiro, 1923; Table 1). Noble (1927) commented that tadpoles of *C. aurita* are cannibalistic. He also dissected a single tadpole of *C. aurita* revealing the presence of tadpoles and ostracods in its diet (Noble, 1927; Table 1). Izecksohn and Carvalho-e-Silva (2001) claim that this species breeds in newly formed puddles along with other explosive breeders, especially microhylids, whose tadpoles serve as food for tadpoles of *C. aurita.*

One species of anuran was confirmed in the diet of post-metamorphic *Ceratophrys aurita,* the microhylid *Hyophryne histrio* (Targino and Wild, 2009). Although there has been a report of an additional anuran species, *Trachycephalus* cf. *mesophaeus,* it cannot be confirmed (see Solé et al., 2010). To this, we add that seven individuals of *Chiasmocleis* sp. (snout–vent length [SVL] = 18.5–9.0 mm) were found (along with the single *Hyophryne histrio* of Targino and Wild, 2009) in the stomach of a single juvenile specimen (SVL = 55.3 mm) from Nova Viçosa municipality (17°52'S, 39°23'W) in the southern part of the State of Bahia, Brazil (MNRJ 19030). Dissection of this specimen and two additional individuals (MNRJ 19031, KU 92740) revealed that arthropods, especially ants (Formicidae) were the most commonly encountered prey (Tables 3 and 4). Izecksohn and Carvalho-e-Silva (2001) report that the prey of *C. aurita* are usually vertebrates, such as amphibians, small birds or small mammals. Feio et al. (2008) mention the prey of *C. aurita* to be small vertebrates such as other amphibians, snakes, and rodents.

Ceratophrys calcarata

We did not find any information on the diet of the tadpoles of *Ceratophrys calcarata.* Prior to this study, the only known prey item of *C. calcarata* was crickets fed to a captive individual while describing pedal luring behavior (Murphy, 1976). We found that arthropods, particularly coleopterans, contributed the largest proportion numerically to the diet of *C. calcarata* (*n* = 2; KU 144966, 207528), followed by vertebrates, which included an unidentified rodent and reptile (Tables 3 and 4).

Ceratophrys cornuta

Captive tadpoles of *Ceratophrys cornuta* were observed consuming five native species of tadpoles (Table 1; Duellman and Lizana, 1994), but nothing is known of their diet under natural conditions.

The study by Duellman and Lizana (1994) of *C. cornuta* in the Peruvian Amazon provides the most comprehensive and detailed study of the diet of any ceratophryid. In their examination of 72 stomachs, ants, and then beetles, had the greatest proportion numerically, while vertebrates, especially anurans and mammals, contributed

Table 1. A compilation of the known prey of the species of Ceratophryidae compiled from field observations or specimen dissections (including the specimens dissected for this study). All species of anuran prey are post-metamorphic frogs unless otherwise specified. Species names follow Frost (2014). Life stage abbreviations: T = tadpole; PM = post-metamorphosis.

Species	Life Stage	Prey	Reference
Ceratophrys aurita	T	*Ceratophrys aurita* tadpoles	Noble, 1927
		Hyla sp. tadpole	
		Unidentified tadpoles	
		Ostracoda	
	PM	*Hyophryne histrio*	Targino and Wild, 2009
		Trachycephalus cf. *mesophaeus*	Solé et al., 2010
		Chiasmocleis sp.	This study
		Acarina	
		Formicidae	
		Hymenoptera	
		Ixodidae	
		Orthoptera	
		Unidentified reptile	
		Unidentified vertebrate	
		Unidentified anuran	
		Unidentified arthropod	
		Amphibians	Izecksohn and Carvalho-e-Silva, 2001
		Small birds	
		Small mammals	
		Amphibians	Feio et al., 2008
		Snakes	
		Rodents	
Ceratophrys calcarata	PM	Coleoptera adult	This study
		Formicidae	
		Unidentified reptile	
		Unidentified arthropod	
		Unidentified rodent	
Ceratophrys cornuta	PM	Orthoptera	Duellman, 1978
		Araneae	
		Edalorhina perezi	
		Leptodactylus dydimus	Chávez et al., 2011
		Plica plica	
		Oligochaeta	Duellman and Lizana, 1994
		Gastropoda	
		Crustacea	
		Aranea	
		Acarina	
		Miriapoda	
		Orthoptera	
		Homoptera	
		Heteroptera	
		Diptera	
		Diptera larvae	
		Formicidae	
		Hymenoptera	
		Coleoptera adult	
		Coleoptera larva	
		Unidentified arthropod	
		Rhinella margaritifera	
		Pristimantis toftae	
		Hamptophryne boliviana	
		Dendropsophus parviceps	
		Scinax ruber	
		Hypsiboas punctatus	
		Ptychoglossus brevifrontalis	
		Anolis fuscoauratus egg	
		Unidentified snake	
		Oecomys bicolor	
		Unidentified mice	
		Oryzomyine rodent	This study

Species	Life Stage	Prey	Reference
Ceratophrys cranwelli	T	*Phyllomedusa sauvagii* tadpoles	This study
		Anostraca	
		Volvocaceae	Vera Candioti, 2005
		Crustacea	
		Desmidiaceae	
		Euglenoids	
		Insecta	
		Nematoda	
		Oligochaeates	
		Rotifers	
		Shell-bearing amoebas	
		Vegetal remants	
		Diatoms	
		Macrophytes	Vera Candioti, 2007
		Tecamebians	
		Ceratophrys cranwelli tadpoles	Gallardo and Varela de Olmedo, 1992
	PM	Anurans	Contreras and Contreras, 1982
		Small mammals	
		Birds	
		Lizards	
		Mollusks	
		Anurans	Norman, 1994
		Dermatonotus muelleri	Wild, 2001
		Leptodactylus bufonius	Schalk, 2010
		Physalaemus albonotatus	Schalk and Montaña, 2011
		Physalaemus biligonigerus	Wild, 2001; Scott and Aquino, 2005
		Leptodactylus sp.	Scott and Aquino, 2005
		Rhinella major	
		Coleoptera adult	
		Phyllomedusa sauvagii	This study
		Unidentified arthropod	
		Formicidae	
		Coleoptera adult	
		Unidentified rodent	
Ceratophrys ornata	T	*Ceratophrys ornata* tadpoles	Noble, 1927, 1931; Cei, 1980
		Tadpoles	Gallardo, 1987b;
		Small crustaceans	Gallardo and Varela de Olmedo, 1992
	PM	Small vertebrates	Cei, 1980; Gallardo, 1987a
		Arthropods	
		Ceratophrys ornata	Gallardo, 1987b;
		Amphibians	Gallardo and Varela de Olmedo, 1992
		Lizards	
		Snakes	
		Juvenile birds	
		Rodents	
		Arthropods	
		Gastropoda-slugs and snails	
		Amphisbaena darwini	Gallardo and Varela de Olmedo, 1992
		Coleoptera	Basso, 1990
		Araneae	
		Isopoda	
		Formicidae	
		Gastropoda	
		Hemiptera	
		Frogs	
		Snakes	
		Birds	
		Rodents	
		Gastropoda	This study
		Unidentified anuran	
		Unidentified arthropod	
		Unidentified fish	
		Unidentified rodent	

Species	Life Stage	Prey	Reference
Chacophrys pierottii	PM	*Physalaemus* spp.	Vellard, 1948
		Leptodactylus spp. juveniles	
		Chacophrys pierottii	Cei, 1955, 1980; Blair, 1976;
		Anurans	Norman, 1994
		Apidae	Pueta and Perotti, 2013
		Formicidae	
		Unidentified Hymenoptera	
		Curculionidae	
		Dytiscidae	
		Heteroceridae	
		Elateridae	
		Tenebrionidae	
		Coccinelidae	
		Pentatomidae	
		Unidentified Hemiptera	
		Diptera adult	
		Diptera larvae	
		Araneae	
		Scorpionidae	
		Lepidoptera larvae	
		Unidentified insect larvae	
		Unidentified anuran	
		Chacophrys pierottii	
		Coleoptera adult	This study
		Coleoptera larva	
		Hemiptera	
		Insect larva	
		Unidentified vertebrate	
		Unidentified arthropod	
Lepidobatrachus asper	PM	*Rhinella major*	Budgett, 1899; Gadow, 1909
		Frogs	Reig and Cei, 1963
		Insects	
		Lepidobatrachus asper	Cei, 1958; Reig and Cei, 1963; Cochran, 1961
		Arthropods	Cei, 1980; Gallardo, 1987a; Gallardo and Varela de Olmedo, 1992
		Small vertebrates	
		Coleoptera adult	Reig and Cei, 1963; Cei, 1980; This study
		Gastropoda	Norman, 1994
		Anurans	
		Aquatic Coleoptera	Sugai et al., 2013
		Terrestrial Coleoptera	
		Araneae	
		Acari	
		Blattodea	
Lepidobatrachus laevis	T	Unidentified tadpoles	Parker, 1931
		Clam shrimp	
		Coleoptera	
		Unidentified aquatic insect	
	PM	Athropods	Gallardo and Varela de Olmedo, 1992
		Small vertebrates	
		Gastropoda	Norman, 1994
		Anurans	
		Rhinella major	Scott and Aquino, 2005
		Pseudis paradoxa	
		Dermatonotus muelleri	
		Physalaemus biligonigerus	
		Physalaemus albonotatus	
		Leptodactylus spp.	
		Unidentified anuran	
		Arthropoda	
		Gastropoda	
		Gastropoda (*Pomacea*)	Faivovich pers. comm.
		Coleoptera adult	This study
		Unidentified arthropod	

Species	Life Stage	Prey	Reference
Lepidobatrachus llanensis	T	Hemiptera larvae	Cei, 1968
		Notostraca	
		Diatoms	Vera Candioti, 2007
		Crustaceans	
		Unidentified tadpoles	
	PM	Oligocheates	Hulse, 1978
		Eubranchipoda	
		Unidentified tadpoles	
		Unidentified anurans	
		Carabidae	
		Belostomatidae nymphs	
		Hymenoptera	
		Lepidobatrachus llanensis	
		Pleurodema guayapae	
		Lepidoptera	
		Coleoptera	
		Gastropoda	
		Anisoptera nymphs	
		Leptodactylus bufonius	
		Notonectidae	
		Scarabidae	
		Araneae	
		Diptera	
		Arthropods	Gallardo and Varela de Olmedo, 1992
		Small vertebrates	

the most volumetrically. Duellman and Lizana (1994) also examined prey frequency across a range of size classes, finding ants were again the most frequent prey item, but particularly for juveniles and adult males. This study also documented that every age class of this species consumes anurans. A range of prey items has been documented in the diet of *C. cornuta,* ranging from arthropods like orthopterans and hymenopterans to vertebrates such as lizards and mammals (Table 1). It has been reported that captive individuals in the field showed a clear preference for *Rhinella margartifera* over other offered native frog species and non-rainforest cockroaches in the Peruvian Amazon (W.W. Lamar, pers. comm.). We add that a medium-sized (ca. 50–90 g) oryzomyine rodent (*Euryoryzomys* or *Hylaeamys*) was observed being eaten alive by an adult *C. cornuta* at Reserva Amazonica in the Peruvian Amazon (Fig. 1A).

Ceratophrys cranwelli

The tadpole diet of *Ceratophrys cranwelli* is the best documented for any ceratophryid species. Cannibalism by *C. cranwelli* tadpoles has been reported by Gallardo and Varela de Olmedo (1992). Previous studies by Vera Candioti (2005, 2007) on seven tadpole specimens documented that Volvocaceae, insects, and crustaceans comprised the largest proportion of the diet of larval *C. cranwelli.* The tadpoles readily consumed tadpoles of *Pleurodema borelli* in captivity (Vera Candioti 2005; 2007), although we add that they consume tadpoles in the wild. On 23 March 2011 at 14:15 h, one of us (CMS) observed a *C. cranwelli* tadpole that had recently captured a fairy shrimp (Crustacea: Anostraca) in shallow water along the edge of a temporary pond. The tadpole had captured the fairy shrimp head-first and proceeded to shear off the head and consume it. The tadpole then proceeded to shear off smaller bits from the body of the fairy shrimp until it had been completely consumed. The tadpole then swam to a deeper part of the pond. The same day at 21:00 h while observing a small school of ten *Phyllomedusa sauvagii* (Hylidae) tadpoles slowly grazing in a temporary pond along the water's surface, CMS observed a *C. cranwelli* tadpole emerge from below and grasp the venter of a *P. sauvagii* tadpole. The *C. cranwelli* tadpole shook the *P. sauvagii* tadpole vigorously and proceeded to disembowel it, after which the *C. cranwelli* tadpole swam to deeper water. The *C. cranwelli* tadpole did not return to consume the *P. sauvagii* tadpole.

Both field observations and dissections have documented a wide variety of anurans and other vertebrates in the diet of post-metamorphic *Ceratophrys cranwelli* (Table 1; Fig. 1B). Here we add that on 23 March 2011 at 21:30 h, one of us (CMS) observed a metamorph *C. cranwelli* (SVL = 30 mm) consuming a recently metamorphosed *P. sauvagii* along the edge of a temporary pond. The *Phyllomedusa sauvagii* still possessed a large tail-bud and had an orange-striped color pattern on its thighs and groin (Cei, 1980), suggesting that the individual had emerged from the nearby pond (approximately 20 cm away) that night. As in other observed predation events (Schalk, 2010; Schalk and Montaña, 2011), the prey item was still alive as it was being consumed and made multiple attempts to force itself from the mouth of the *C. cranwelli.* During the

Table 2. A compilation of the known prey of the species of Ceratophryidae consumed while in captivity or as part of a feeding experiment using native potential prey. Studies conducted with non-native potential prey are not included. All species of anuran prey are post-metamorphic frogs unless otherwise specified. Species names follow Frost (2014). Life stage abbreviations: T = tadpole; PM = post-metamorphosis.

Species	Life Stage	Prey	Reference
Ceratophrys aurita	T	*Ceratophrys aurita* tadpoles	Miranda-Ribeiro, 1923
		Leptodactylus sp. tadpoles	
		Leptodactylus latrans tadpoles	
	PM	Young chickens	Miranda-Ribeiro, 1920
Ceratophrys cornuta	T	*Dendropsophus koechlini* tadpoles	Duellman and Lizana, 1994
		Ctenophryne geayi tadpoles	
		Chiasmocleis ventrimaculata tadpoles	
		Dendropsophus leucophyllatus tadpoles	
		Elachistocleis ovalis tadpoles	
	PM	*Rhinella margaritifera*	W.W. Lamar pers. comm.
Ceratophrys cranwelli	T	*Pleurodema borelli* tadpoles	Vera Candioti, 2005, 2007
Ceratophrys ornata	T	*Hypsiboas pulchellus* tadpoles	Natale et al., 2011
		Scinax squalirostris tadpoles	
		Odontophrynus americanus tadpoles	
		Leptodactylus latrans tadpoles	
		Rhinella arenarum tadpoles	
		Rhinella fernandezae tadpoles	
		Ceratophrys ornata tadpoles	Fernández and Fernández, 1921
		Frogs	Gadow, 1909
		Ceratophrys ornata	
	PM	Orthoptera	Gallardo, 1974
		Ceratophrys ornata	
		Rhinella arenarum	
		Mice	
		Dendropsophus minutus	Braun et al., 1980
		Dendropsophus sanborni	
		Hypsiboas leptolineatus	
		Hypsiboas pulchellus	
		Leptodactylus gracilis	
		Leptodactylus latinasus	
		Leptodactylus latrans	
		Odontophrynus americanus	
		Physalaemus gracilis	
		Pseudis minuta	
		Rhinella arenarum	
		Rhinella crucifer	
		Rhinella dorbignyi	
		Rhinella fernandezae	
		Scinax fuscovarius	
		Scinax squalirostris	
		Unidentified hylid	
		Liophis jaegeri	
		Liophis poecilogyrus	
Lepidobatrachus laevis	T	*Lepidobatrachus laevis* tadpoles	Ruibal and Thomas, 1988
	PM	*Rhinella schneideri*	Scott and Aquino, 2005
		Lepidobatrachus laevis	
		Leptodactylus bufonius	
		Leptodactylus chaquensis	
		Leptodactylus fuscus	
		Phyllomedusa hypochondrialis	
		Phyllomedusa sauvagii	

Table 3. Number of food items found from dissections in seven species of frogs of the family Ceratophryidae. MW = mouth width; SVL = snout-vent length.

	Ceratophrys				*Chacophrys*	*Lepidobatrachus*	
	aurita	***calcarata***	***cranwelli***	***ornata***	***pierottii***	***asper***	***laevis***
No. stomachs	3	2	2	2	9	2	1
SVL (mm)	47.5–104.5	62.2–62.6	53.9–71.5	52.3–79.6	29.1–38.3	43.9–56.6	46.2
MW (mm)	29.8–68.6	38.5–43.1	29.6–48.8	36.4–46.9	17.0–19.9	29.4–33.6	30
Acarina	2						
Chiasmocleis sp.	8						
Coleoptera adult		10	3		13	2	2
Coleoptera larva					16		
Detritus					2	1	1
Formicidae	32	2	1		2		
Gastropoda				1			
Hyophryne sp.	1						
Hemiptera					1		
Hymenoptera	2						
Insect larva					1		
Isoptera	2						
Ixodidae	1						
Lepidoptera larva					5		
Orthoptera	2						
Plant matter	1	1	1	1	4		1
Stone							1
Unidentified reptile	1	1		1			
Unidentified vertebrate	1				4		
Unidentified anuran	1			1			
Unidentified arthropod	2	2	2	1	8		1
Unidentified fish				1			
Unidentified rodent		1	2	1			
Unknown	2		1	1	4		
Total	58	17	10	8	60	3	6

brief periods when the *P. sauvagii* rested between escape attempts, the *C. cranwelli* used its hands and the ground to force the *P. sauvagii* further into its mouth. After 25 minutes, the *C. cranwelli* completely ingested the *P. sauvagii*. This prey species has been rejected by other anurophagous frogs in the region (Scott and Aquino, 2005). The *C. cranwelli* was kept overnight to observe if there were any adverse effects of the *P. sauvagii* consumption on the *C. cranwelli*. The *P. sauvagii* was still retained by the *C. cranwelli* the following morning and the *C. cranwelli* was then released the following night.

These observations show the additional detail that *C. cranwelli* is anurophagous at all age classes, including tadpoles, metamorphosed individuals (see observation above; Schalk, 2010), and adults (Schalk and Montaña, 2011). However, we cannot comment on the proportion of these prey items at various age classes, because these are based off of single observations. Nonetheless, in the

Table 4. Numerical proportions of general prey categories found from dissections in seven species of frogs of the family Ceratophryidae. MW = mouth width; SVL = snout-vent length.

	Ceratophrys				*Chacophrys*	*Lepidobatrachus*	
	aurita	***calcarata***	***cranwelli***	***ornata***	***pierottii***	***asper***	***laevis***
No. stomachs	3	2	2	2	9	2	1
SVL (mm)	47.5–104.5	62.2–62.6	53.9–71.5	52.3–79.6	29.1–38.3	43.9–56.6	46.2
MW (mm)	29.8–68.6	38.5–43.1	29.6–48.8	36.4–46.9	17.0–19.9	29.4–33.6	30
Arthropods (%)	74.1	82.4	60.0	12.5	76.7	66.7	50.0
Gastropods (%)	0.0	0.0	0.0	12.5	0.0	0.0	0.0
Vertebrates (%)	20.7	11.8	20.0	50.0	6.7	0.0	0.0
Other (%)	5.2	5.9	10.0	25.0	16.7	33.3	50.0

two post-metamorphic individuals we dissected, arthropods were the most common prey item, though we found for the first time evidence of this species having consumed a rodent (Tables 3 and 4). This species has been reported to consume non-native prey items, consisting of both invertebrates and vertebrates, in captivity (Grayson et al., 2005).

Ceratophrys ornata

Other than several references commenting on their cannibalistic tendencies (Fernández and Fernández, 1921; Noble, 1927, 1931; Cei, 1980), there is little other information on the diet of tadpoles of *Ceratophrys ornata* in nature (Table 1). In their laboratory study, Natale et al. (2011) offered as food tadpoles of seven different species of frogs (Table 2) known to share ponds with *C. ornata* in nature, all of which were consumed. These authors argued that the occurrence in nature of cannibalism by *C. ornata* larvae is likely rare because of low population densities of these tadpoles relative to the tadpoles of other synchronously reproducing frogs with high reproductive potential.

Gallardo (1974) fed captive adult *C. ornata* native orthopterans, mice, and two species of frogs including *C. ornata* (Table 2), but also non-native gastropods and beetles. Cei (1980) commented that adult *C. ornata* can consume small arthropods and small vertebrates, as did Gallardo (1987a), but he did not provide any further details. In a feeding study over the course of 17 months, Braun et al. (1980) fed a single captive individual 17 species of anurans and two species of snakes (Table 1). Gallardo (1987b) and Gallardo and Varela de Olmedo (1992) report post-metamorphic individuals feeding on wide variety of vertebrates, plus arthropods and molluscs, and also reported cannibalism. The most complete examination of the natural diet of *C. ornata* is that of Basso (1990) who examined the contents of 34 stomachs and determined that anurans were the most important of ten different prey categories found, both volumetrically (78.50%) and numerically (45.53%). Basso (1990) concludes that *C. ornata* is an anuran specialist, but noted that other vertebrates (birds, rodents, and a snake) and a variety of invertebrates (mostly coleopterans, isopods, and ants) were also consumed. Dissection of two specimens revealed that, numerically, vertebrates were the most frequent food items, though we did find both gastropod and arthropod invertebrates (Tables 3 and 4).

Chacophrys pierottii

As previously mentioned, tadpoles of *Chacophrys pierottii* lack the carnivorous traits of *Ceratophrys* and *Lepidobatrachus* and is a member of the benthic ecomorphological guild (Altig and McDiarmid, 1999; Quinzio et al., 2006). Polis and Myers (1985:103, Table 2) indicate in their table that the tadpoles of *C. pierottii* are cannibalistic citing Cei (1955) and Blair (1976); however, neither of these citations specifically mention tadpoles of *C. pierottii* being cannibalistic. Furthermore, Blair (1976) only makes the general assertion about "ceratophrynids" that "Both larvae and adults are carnivorous and cannibalistic" citing Cei (1955), Reig and Cei (1963), and "my data". We found no additional information on their diet in the wild.

Multiple authors have documented anurans in the diet of post-metamorphic *C. pierottii* (Vellard, 1948; Norman, 1994). In their study on the diet of juvenile *Chacophrys pierottii,* Pueta and Perotti (2013) revealed that hymenopterans and coleopterans were the dominant prey numerically and displayed the highest index of relative importance, whereas anurans and hymenopterans were the dominant prey volumetrically. Other prey items included scorpions, spiders, dipterans, and insect larvae (Pueta and Perotti, 2013; Table 1). Cannibalism in juvenile *C. pierottii* was also documented (Pueta and Perotti, 2013). Besides the Pueta and Perotti (2013) study, there are only anecdotal reports that post-metamorphic individuals of this species are highly cannibalistic (Table 1). In the nine individuals dissected, arthropods comprised the majority of the diet, particularly larval and adult coleopterans, though we also found evidence of an unidentifiable vertebrate food item (Tables 3 and 4).

Lepidobatrachus asper

We did not find any information on the diet of *Lepidobatrachus asper* tadpoles.

All prior knowledge on the diet of post-metamorphic *L. asper* has been provided via anecdotes. Budgett (1899) commented that this species primarily feeds upon "*Bufo granulosus*" (= *Rhinella major,* Bufonidae). Other authors have documented cannibalism in this species and even more recent comments include frogs, arthropods, and gastropods as prey items (Table 1). In the four juvenile specimens dissected by Sugai et al. (2013), all the stomachs were empty but the intestines contained a few arthropods, plus plant material and sand particles which was considered to incidental to the ingestion of arthropod prey (Table 1). In the two specimens dissected, the only discernible items were larval coleopterans and detritus (Tables 3 and 4).

Lepidobatrachus laevis

Tadpoles of *Lepidobatrachus laevis* displayed cannibalism and were observed consuming non-native fish

(*Poecilia* sp., *Carassius* sp.) in captivity (Ruibal and Thomas 1988; Table 2). Parker (1931) dissected a single wild caught individual to reveal that tadpoles were the most frequently consumed prey, but also found that it consumed other small aquatic invertebrates (Table 1).

In the Paraguayan Chaco, at least six species of anurans have been found in the diet of post-metamorphic *L. laevis* (Table 1). Although feeding experiments by Scott and Aquino (2005) revealed that more species are palatable (Table 2), gastropods were the most frequent food item found in the stomachs. Other reported food items include arthropods, small vertebrates, and gastropods (Gallardo and Varela de Olmedo, 1992; Norman, 1994; Table 1). In our dissection of a single individual, we found arthropods as being the most frequent prey item (Tables 3 and 4). At Laguna Yema Formosa in Argentina, numerous *L. laevis* were collected that had their stomachs completely full with single individuals of freshwater snails of the genus *Pomacea* (J. Faivovich, pers. comm.). After leaving several adult individuals overnight in a sink, several opercula were found that were presumed to have been regurgitated. A few dissected specimens showed the snail shell to be perforated with numerous tiny holes, as if the gastric acids had started to dissolve the calcium carbonate of the shell (J. Faivovich, pers. comm.).

Lepidobatrachus llanensis

Aquatic invertebrates were the only food items found in the *Lepidobatrachus llanensis* tadpole specimens dissected by Cei (1968), while Vera Candioti (2007) found that tadpoles were the most frequent prey item, followed by crustaceans, and a negligible amount of diatoms in the four specimens she dissected (Table 2).

Dissection of 33 post-metamorphic individuals of *L. llanensis* from Argentina revealed that aquatic oligochaetes were the most common food item by both frequency and volume (Hulse, 1978; Table 1). However, this species did consume a number of invertebrates and vertebrates, specifically anurans, such as *Leptodactylus bufonius, Pleurodema guayapae,* as well as its own species (Table 1).

DISCUSSION

One general statement can certainly be said about the diet of frogs of the Ceratophryidae, in spite of their voracious feeding reputation much remains to be learned about what they eat during any of their life stages—in fact, we were unable to find any information at all for one-fourth of the species in the family (*Ceratophrys joazeirensis, C. stolzmanni,* and *C. testudo*). Many of the reports we did find on ceratophryid diet were anecdotal observations of only a few or individual specimens and often in captivity. Very few studies (Hulse, 1978; Basso, 1990; Duellman and Lizana, 1994; Pueta and Perotti, 2013) actually attempted to quantify the diet of naturally occurring ceratophryids. It seems the reputation of ceratophryid frogs as voracious megalophagous carnivores and cannibals is a generalization that has grown from very limited data. In fact, cannibalism by adults has only been reported for five of the twelve species, and by tadpoles for only four species. Yet we have found several authors that simply state, or at least imply, without data and often without a citation, that *all* ceratophryids are megalophagous and cannibalistic, and even when citations are given they concern only one or a few of the species. For example, the frequently referenced Blair (1976) states that "The ceratophrynids are much more cannibalistic than *Scaphiopus.* Both larvae and adults are carnivorous and cannibalistic (Cei, 1955b [Cei, 1955 of the present paper]; Reig and Cei, 1963; my data)." and "Adult *Chacophrys pierottii* are extremely voracious cannibals; one of these can quickly ingest another individual of its own body size." However, "Cei, 1955b" (herein cited as Cei, 1955) only gives observations of cannibalism in adult *Ch. pierottii,* Reig and Cei (1963) only state that *L. asper* eats other frogs and insects and will cannibalize, and Blair provides none of his "own data." Likewise, Fabrezi and Quinzio (2008) state "Adults of ceratophryines are megalophagous and are cannibals (Ruibal and Thomas, 1988; Hanken, 1993)." But Ruibal and Thomas (1988) only report cannibalism in *L. laevis* from captive individuals and state, without reference, "… *Ceratophrys* which has predatory carnivorous larvae." and Hanken (1993) only cites Ruibal and Thomas (1988) and gives no other source or data for his generalizations of feeding across all species of ceratophryids. So, herein we have attempted to distil the limited data that exists from the unsubstantiated generalizations, meanwhile adding additional information for eight species, including the first report on the diet of *C. calcarata*.

Tadpole diet

Of the 12 species of ceratophryids, tadpole diet data were known for only half (four species of *Ceratophrys* and two species of *Lepidobatrachus*). We added information for only one of these, *C. cranwelli*. The most commonly reported item in the tadpole diet of these species of *Ceratophrys* were tadpoles of other species of Bufonidae, Hylidae, Leptodactylidae, Microhylidae, and Odontophrynidae. Two species, *C. aurita* and *C. ornata,* also have multiple reports of tadpole cannibalism in nature. Likewise, both of the species of *Lepidobatrachus* (*L. laevis* and *L. llanensis*), for which we found tadpole diet data, consumed tadpoles as well (reported as unidentified) and *L. laevis* exhibited cannibalism, albeit in the laboratory (Ruibal and Thomas,

Table 5. Major groups of vertebrates (left) and amphibians (right) as prey of post-metamorphic individuals of species of Ceratophryidae. All instances are observations in nature except those indicated by a boldface **X,** which were in captivity of part of a feeding experiment using native potential prey.

Predator Species of the Ceratophryidae	Major vertebrate groups as prey					Amphibian groups as prey							
	Amphibia	Reptilia	Mammalia	Aves	Actinopterygii	Tadpoles	Cannibalism	Microhylidae	Hylidae	Leptodactylidae	Bufonidae	Craugastoridae	Odontophrynidae
Ceratophrys													
aurita	X	X	X	X				X	X				
calcarata		X	X										
cornuta	X	X	X					X	X	X	X	X	
cranwelli	X	X	X	X				X	X	X	X		
ornata	X	X	X	X	X		X		**X**	**X**	**X**		**X**
Chacophrys													
pierottii	X						X			X			
Lepidobatrachus													
asper	X						X						
laevis	X						**X**	X	X	X	X		
llanensis	X					X	X			X			

1988; E.R. Wild, pers. observ.). Although there are no direct data regarding the diet of *Chacophrys pierottii* tadpoles, due to its morphology as a Type IV tadpole (Orton, 1953) of the benthic ecomorphological guild (Altig and McDiarmid, 1999), they are not expected to prey on tadpoles nor be cannibalistic, reports to the contrary notwithstanding (i.e., Polis and Myers, 1985).

It appears that tadpoles of the species of *Ceratophrys* and *Lepidobatrachus* prefer a tadpole diet, but whether they selectively choose various taxa or not is unclear. It is, however, noteworthy that *C. cranwelli* readily consumed, when offered, two species of bufonid tadpoles since these are generally considered toxic to vertebrates (Wassersug, 1971; Alford, 1999). Cannibalism among ceratophryid tadpoles is widely alleged, so it was surprising to find data limited to just five species, two of which remain questionable at best. The claim of cannibalism in *Chacophrys pierottii* is due to broad generalizations regarding the entire family that have been perpetuated (e.g., Blair, 1976; Reig and Cei, 1963; Polis and Myers, 1985) and remains in doubt. One of the most frequently cited papers for cannibalism in tadpoles of the Ceratophryidae is Reig and Cei (1963), however, they only report cannibalism by *L. laevis* based on captive individuals. For the other three species (*C. aurita, C. cranwelli,* and *C. ornata*), there is no conclusive evidence whether this cannibalism is intentional or that it is the incidental consumption of just another tadpole. Either way, this cannibalism serves as a strategy for accelerating development in the temporary aquatic habitats (Crump, 1983) that most ceratophryids utilize, and certainly does so for the three cannibalistic species identified here that reside in the Gran Chaco. As a strategy for accelerating development, cannibalism assures an abundant local food source, it eliminates competitors, and provides additional thyroxin, all of which are known to contribute to more rapid development and metamorphosis (Pfennig, 1992; Wild, 1997b).

Since the diet of the tadpoles of *Ceratophrys cranwelli* is the best documented for any ceratophryid species, our findings for this species may be particularly enlightening to the nature of all *Ceratophrys* tadpoles. Our observations provide further evidence as to the predatory nature of tadpoles of *C. cranwelli*. While Vera Candioti (2005) noted that the tadpoles of *C. cranwelli* often engulfed tadpoles of *Pleurodema borelli* whole, our field observations document that these tadpoles will readily attack and consume prey species larger than themselves and appear to not be gape constrained. The additional observations we found documented in the literature also support the predatory nature of these tadpoles. While tadpoles of *Lepidobatrachus* are most likely to be obligate carnivores in the ponds which they inhabit, Vera Candioti (2005) studied the morphology and feeding mechanics of *C. cranwelli* and proposed that they may be facultative carnivores, exhibiting some degree of trophic plasticity. As many of the other species of *Ceratophrys* tadpoles are similar to *C. cranwelli* morphologically (e.g., Duellman and Lizana, 1994; Wild, 1997b), it is likely that these species are also facultative carnivores. Similarly, though the tadpole of *Chacophrys pierottii* is a member of the benthic ecomorphological guild, recent research of similar tadpole ecomorphs has suggested that they may be omnivores or even carnivores (Altig et al., 2007).

Our knowledge of the functional role of the ceratophryid tadpole is based on extremely small sample sizes, with the largest being seven individuals, and often

limited to individuals collected from a single pond. Furthermore, the resources that these tadpoles utilize are likely to vary across both pond type and season (Schalk, unpubl. data). We recognize that specimen dissections are time-consuming and may provide only a snapshot of the prey items in the gut of these species, so we suggest that stable isotopes be utilized to understand the functional role of these species (*sensu* Altig et al., 2007), in particular they may be useful for those species that may be inherently plastic in their trophic ecology (i.e., *Chacophrys pierottii* and *Ceratophrys* spp.).

Post-metamorphic diet

Prior to this study, adult diet data were known for eight species of ceratophryids; we were unable to find any previous information on the post-metamorphic diets of *Ceratophrys calcarata, C. joazeirensis, C. stolzmanni,* and *C. testudo*. However, we do add here, for the first time, data on the diet of post-metamorphic *C. calcarata*. All these species have been documented to eat vertebrates in nature and all, except *C. calcarata,* consumed frogs (primarily Bufonidae, Hylidae, Leptodactylidae, and Microhylidae, but there are also instances of Craugastoridae and Odontophrynidae). However, the lack of evidence of anurophagy in *C. calcarata* may simply be due to our small sample size. One emergent pattern we observed is that prey items of the other major vertebrate groups (Reptilia, Mammalia, Aves, Actinopterygii) were only found among species of the genus *Ceratophrys,* with each species having prey from at least two of these groups (most often Reptilia and Mammalia; Table 5). On the other hand, none of the species of *Lepidobatrachus* or *Chacophrys pierottii* had any prey items from among these non-anuran vertebrate groups. This may be because of the terrestrial versus aquatic nature of *Ceratophrys* and *Lepidobatrachus,* respectively, yet it does not explain the absence of non-anuran vertebrates in *Chacophrys* (terrestrial) or the only fish item being found in *C. ornata* (terrestrial). The most comprehensive study of the diet of *Ch. pierottii* only focused on post-metamorphic juveniles (Pueta and Perotti, 2013), which may experience constraints imposed by their limited gape size (as compared to adults) and are unable to consume larger vertebrate prey. Furthermore, cannibalism by adults was documented in only one species of *Ceratophrys* (*C. ornata*) but observed in all species of *Lepidobatrachus* and *Ch. pierottii*. Adults of one species (*L. llanensis*) had tadpoles in its diet, which is not a surprise because of their aquatic nature.

Species of ceratophryids are by no means limited to vertebrate prey, and we realize that our compilation is likely to be biased to the larger, more easily observable prey items. In fact, all of the observations from feeding experiments or captive individuals used only vertebrates as prey, which likely perpetuated the idea that these species primarily feed upon vertebrates. However, the few thorough and detailed studies of post-metamorphic diet of these species (i.e., *Lepidobatrachus llanensis* by Hulse, 1978; *Ceratophrys ornata* by Basso, 1990; *C. cornuta* by Duellman and Lizana, 1994; *Chacophrys pierottii* by Pueta and Perotti, 2013) show the extremely broad spectrum of items in the diet of these frogs, ranging from invertebrates to vertebrates. For many of the other ceratophryid species, the largest proportion of the information available on their diet come from laboratory feeding studies. While these laboratory studies address the question of palatability of potential prey species, they do not provide information of which species contribute an important portion of their diet under natural conditions.

Generalities that can be made: all species of *Ceratophrys* that have been studied for diet appear to be generalist, opportunistic feeders, as demonstrated for *C. cornuta* (Duellman and Lizana, 1994). But there has yet to be any study on prey availability in their natural habitats, which is needed to confirm this suspicion. Certainly, there are many more small prey items in their diet than their reputation suggests, and although they do consume larger prey, including vertebrates nearly of their own size, these seem to be opportunistic encounters. For those species without data, phylogenetically they would be expected to have similar diets.

Our review also highlights some notable observations that deserve comment. The first of these is the observation of pedal luring behavior by adult *Ceratophrys aurita* (Izecksohn and Carvalho-e-Silva, 2001), which is only the third report of this behavior among ceratophryids, the other species being *C. calcarata* (Murphy, 1976) and *C. ornata* (Radcliffe et al., 1986). This behavior might be more widespread but perhaps phylogenetically limited to *Ceratophrys*. The second observation that deserves comment are the multiple reports on the aggressive nature of these species during reproductive bouts. Female *C. cranwelli* have been observed biting male conspecifics during multiple mating attempts (Silva et al., 2014), and even after being amplexed, female *C. cranwelli* have been observed consuming or attempting to capture heterospecific anurans (see photograph in Schalk and Montaña, 2011, and report by Silva et al., 2014). Whether aggressive interactions between males and females are more widespread in other species of ceratophryids, and whether predation of males by females actually occurs, is unknown but deserves further investigation. The last observation that deserves comment is the evidence of durophagy (consumption of hard-bodied food items) via the consumption of large freshwater snails by post-metamorphic *Lepidobatrachus laevis* (J. Faivovich pers. comm.; Scott and Aquino, 2005). Whether or not snails are a regular part of *L. laevis* diet, or if other species of *Lepidobatrachus* consume snails as well, the digestive abilities of *L. laevis* and the nutritional

value of these prey are interesting and warrants further investigation.

Changes during ontogeny

The ontogenetic niche shift associated with amphibian metamorphosis is a well-studied ecological phenomenon (Wilbur, 1980; Werner and Gilliam, 1984), but fewer studies have examined the niche shifts occurring in the post-metamorphic life stage from metamorph to adult. Whereas there is a fair amount known about the ontogenetic changes in morphology associated with feeding in ceratophryids (Fabrezi and Emerson, 2003; Wild, 1997a, b), these changes have yet to be correlated with changes in diet. Body size is an important factor influencing a species' trophic ecology, such as morphological constraints on prey size, as well as its vulnerability to predators, competitors, and physiological constraints, which can influence the selection of ambush sites. Some ceratophryids undergo over a four-fold increase in body size during post-metamorphic ontogeny (Wild, 1997b), and, therefore, we expect ontogenetic niche shifts to be pervasive in these species. For example, in the Bolivian Chaco, *Ceratophrys cranwelli* exhibited an ontogenetic shift in ambush sites, with metamorphs and adults selecting different sites (Schalk, unpubl. data). Even after our review and addition of observations, comments about the ontogenetic changes in diet remain speculative because so few studies present diet data across multiple size classes and with adequate sample sizes. Future efforts should attempt to examine the diet across different size classes.

CONCLUSION

In spite of the voracious feeding behavior and the many generalizations of megalophagy and cannibalism attributed to frogs of the Ceratophryidae, the few thorough studies on diet in nature suggest that most are likely generalist, opportunistic predators and that a clear understanding of their diet has yet to be achieved. Certainly, most ceratophryids are capable of eating relatively large food items, but many other items are also found in their diet. Questions remain, such as, what feeding strategy do these frogs employ in choosing prey? Are they indeed choosing large items, or are they sampling preying opportunistically on anything they encounter? Similar questions can be posed regarding the larval stage, as even less is known about the diet of the tadpoles of these species in their breeding ponds. These species are cryptic and, thus, difficult to locate in the environment, making collecting and opportunistic encounters difficult. Future efforts should attempt to document the diet of all life stages of these frogs, especially for those species for which data are completely lacking.

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REFERENCES

Alford R.A. 1999. Ecology: resource use, competition, and predation. Pp. 240–278, in Altig R., McDiarmid R.W. (Eds.), Tadpoles: The Biology of Anuran Larvae. The University of Chicago Press, Chicago.

Altig R., McDiarmid R.W. 1999. Diversity: familial and generic characterizations. Pp. 295–337, in Altig R., McDiarmid R.W. (Eds.), Tadpoles: The Biology of Anuran Larvae. The University of Chicago Press, Chicago.

Altig R., Whiles M.R., Taylor C.L. 2007. What do tadpoles really eat? Assessing the trophic status of an understudied and imperiled group of consumers in freshwater habitats. *Freshwater Biology* 52:386–395. doi:10.1111/j.1365-2427.2006.01694.x

Basso N.G. 1990. Estrategias adaptativas en una comunidad subtropical de anuros. *Cuadernos de Herpetología, Serie Monografías* 1:1–72.

Blair F.W. 1976. Adaptations of anurans to equivalent desert scrub of North and South America. Pp. 197–222, in Goodall D.W. (Ed.), Evolution of Desert Biota. University of Texas Press, Austin.

Braun P.C., Braun C.A.S., Pineda M.D.S. 1980. Observações sobre o comportamento alimentar de *Ceratophrys ornata* (Bell, 1843) em cativeiro. *Revista Brasileira de Biologia* 40:401–403.

Budgett J.S. 1899. Notes on the batrachians of the Paraguayan Chaco, with observations upon their breeding habits and development, especially with regard to *Phyllomedusa hypochondrialis,* Cope. Also a description of a new genus. *Quarterly Journal of Microscopical Science* 42:305–333.

Cei J.M. 1955. Chacoan batrachians in central Argentina. *Copeia* 1955:291–293. doi:10.2307/1440305

Cei J.M. 1958. Geographic isolation and phenotyptic constitution of populations of *Lepidobatrachus asper,* a Neotropical batrachian inhabitant of arid regions. *Evolution* 12:166–172. doi:10.2307/2406027

Cei J.M. 1968. Notes on the tadpoles and breeding ecology of *Lepidobatrachus* (Amphibia: Ceratophryidae). *Herpetologica* 24:141–146.

Cei J.M. 1980. Amphibians of Argentina. *Monitore Zoologico Italiano. Nouva Serie, Monographia* 2:1–609.

Chávez G., Venegas P.J., Lescano A. 2011. Two new records in the diet of *Ceratophrys cornuta* Linneaus, 1758 (Anura: Ceratophryidae). *Herpetology Notes* 4:285–286.

Cochran D.M. 1961. *Living Amphibians of the World*. Doubleday & Company, New York.

Contreras J.R., Contreras A.N.C. de. 1982. Características ecológicas y biogeográficas de la bactracofauna del noroeste el la provincia de Corrientes, Argentina. *Ecosur* 9:29–66.

Crump, M.L. 1983. Opportunistic cannibalism by amphibian larvae in temporary aquatic environments. *The American Naturalist* 121:281–289.

Duellman W.E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. *University of Kansas Museum of Natural History Miscellaneous Publication* 65:1–352.

Duellman W.E., Koechlin J.E. 1991. The Reserva Cuzco Amazonico, Peru: biological investigations, conservation, and ecotourism. *Occasional Papers of the Museum of Natural History, University of Kansas* 142:1–38.

Duellman W.E., Lizana M. 1994. Biology of a sit-and-wait predator, the leptodactylid frog *Ceratophrys cornuta*. *Herpetologica* 50:51–64.

Emerson S.B. 1985. Skull shape in frogs: correlations with diet. *Herpetologica* 41:177–188.

Fabrezi M., Emerson S.B. 2003. Parallelism and convergence in anuran fangs. *Journal of Zoology* 260:41–51. doi:10.1017/S0952836903003479

Fabrezi M., Quinzio S.I. 2008. Morphological evolution in Ceratophryinae frogs (Anura, Neobatrachia): the effects of heterochronic changes during larval development and metamorphosis. *Zoological Journal of the Linnean Society* 154:752–780. doi:10.1111/j.1096-3642.2008.00420.x

Feio, R.N., Santos P.S., Cassini C.S., Dayrell J.S, de Oliveira E.F. 2008. Anfíbios da Serra do Brigadeiro, MG. MG.BIOTA: Boletim Técnico Científico da Diretoria de Biodiversidade do Instituto Estadual de Florestas.

Fernández K., Fernández M. 1921. Sobre la biología y reproducción de algunos batracios Argentinos. I. Cystignathidae. *Anales de la Sociedad Científica Argentina* 91:97–140.

Frost D.R. 2014. Amphibian species of the world: an online reference. Version 6.0. (3 April 2014). Accessible at http://research.amnh.org/herpetology/amphibia/index.html. Accessed 03 April 2014.

Gadow H. 1909. Amphibians and Reptiles. *The Cambridge Natural History* Vol III. MacMillan and Co., London.

Gallardo J.M. 1974. Anfibios de los Alrededores de Buenos Aires. Editorial Universitaria de Buenos Aires, Buenos Aires.

Gallardo J.M. 1987a. Anfibios Argentinos: Guía para su Identificación. Librería Agropecuaria, Buenos Aires.

Gallardo J.M. 1987b. Anfibios y reptiles del Partido de Magdalena (provincia de Buenos Aires). Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires.

Gallardo J.M., Varela de Olmedo E. 1992. Anfibios de la República Argentina: Ecologia y Comportamiento. Fauna de Agua Dulce de la Republica Argentina. PROFADU (CONICET), Buenos Aires.

Grayson K.L., Cook L.W., Todd M.J., Pierce D., Hopkins W.A., Gatten R.E. Jr., Dorcas M.E. 2005. Effects of prey type on specific dynamic action, growth, and mass conversion efficiencies in the horned frog *Ceratophrys cranwelli*. *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology* 141:298–304. doi:10.1016/j.cbpb.2005.05.052

Hanken J. 1993. Model systems versus outgroups: alternative approaches to the study of head development and evolution. *American Zoologist* 33:448–456. doi:10.1093/icb/33.4.448

Hulse A.C. 1978. Food habits of the frog *Lepidobatrachus llanensis* (Amphibia, Anura, Leptodactylidae) in Argentina. *Journal of Herpetology* 12:258–260. doi:10.2307/1563421

Izecksohn E., Carvalho-e-Silva, S.P. 2001. Anfibios do Município do Rio de Janeiro. Editora Universidade Federal Rio de Janeiro, Rio de Janeiro.

Linnaeus C. 1758. Systema Naturae per Regna Tria Naturae Secundum Classes, Ordines, Genera, Species, cum, Characteribus, Differentiis, Synonymis, Locis. Tomus 1. Stockholm.

Lynch J.D. 1982. Relationships of the frogs of the genus *Ceratophrys* (Leptodactylidae) and their bearing on hypotheses of Pleistocene forest refugia in South America and punctuated equilibria. *Systematic Biology* 311:66–179. doi:10.1093/sysbio/31.2.166

Miranda-Ribeiro A. 1920. Algumas considerações sobre o genero *Ceratophrys* e suas especies. *Revista do Museu Paulista* 12:291–304.

Miranda-Ribeiro A. 1923. Observações sobre algumas phases evolutivas de *Ceratophrys* e *Stombus*. *Archivos do Museu Nacional do Rio de Janeiro* 24:201–206.

Murphy J.B. 1976. Pedal luring in the leptodactylid frog, *Ceratophrys calcarata* Boulenger. *Herpetologica* 32:339–341.

Natale G.S., Alcalde L., Herrera R., Cajade R., Schaefer E.F., Marangoni F., Trudeau V.L. 2011. Underwater acoustic communication in the macrophagic carnivorous larvae of *Ceratophrys ornata* (Anura: Ceratophryidae). *Acta Zoologica* 92:46–53. doi:10.1111/j.1463-6395.2009.00445.x

Navarro G., Maldonado M. 2002. Geografia Ecologica de Bolivia: Vegetacion y Ambientes Acuaticos, Centro de Ecologia Difusion Simon I Patino, Santa Cruz de la Sierra.

Noble G.K. 1927. The value of life history data in the study of the evolution of the Amphibia. *Annals of the New York Academy of Sciences* 30:31–128. doi:10.1111/j.1749-6632.1927.tb55359.x

Noble G.K. 1931. *The Biology of the Amphibia*. McGraw-Hill, New York.

Norman D.R. 1994. *Amphibians and Reptiles of the Paraguayan Chaco*. Published by author, San José.

Orton G.L. 1953. The systematics of vertebrate larvae. *Systematic Biology* 2:63–75. doi:10.2307/2411661

Parker H.W. 1931. Reports of an expedition to Brazil and Paraguay in 1926–27, supported by the Trustees of the Percy Sladen Memorial Fund and the Executive Committee of the Carnegie Trust for Scotland. Amphibia and Reptilia. *Journal of the Linnean Society of London* 37:285–289. doi:10.1111/j.1096-3642.1930.tb02070.x

Parsons C.W. 1932. Habits of the toad, *Ceratophrys*. *Nature* 130:279.

Pfennig E.W. 1992. Proximate and functional causes of polyphenism in an anuran tadpole. *Functional Ecology* 6:167–174. doi:10.2307/2389751

Polis G.A., Myers, C.A. 1985. A survey of intraspecific predation among reptiles and amphibians. *Journal of Herpetology* 19:99–107. doi:10.2307/1564425

Pueta M., Perotti M.G. 2013. Feeding habits of juvenile *Chacophrys pierottii* (Ceratophryidae-Ceratophryinae) from northwestern Córdoba province, Argentina. *Herpetological Conservation and Biology* 8:376–384.

Quinzio S.I., Fabrezi M., Faivovich J. 2006. Redescription of the tadpole of *Chacophrys pierottii* (Vellard, 1948) (Anura, Ceratophryidae). *South American Journal of Herpetology* 1:202–209. doi:10.2994/1808-9798(2006)1[202:ROTTOC]2.0.CO;2

Radcliffe C.W., Chiszar D., Estep K., Murphy J.B., Smith H.M. 1986. Observations on pedal luring and pedal movements in leptodactylid frogs. *Journal of Herpetology* 20:300–306. doi:10.2307/1564496

Reig O.A., Cei J.M. 1963. Elucidación morfológico-estadística de las entidades del género *Lepidobatrachus* Budgett (Anura, Ceratophrynidae), con consideraciones sobre la extensión del distrito chaqueño del dominio zoogeográfico subtropical. *Physis* 24:181–204.

Ruibal R., Thomas E. 1988. The obligate carnivorous larvae of the frog, *Lepidobatrachus laevis* (Leptodactylidae). *Copeia* 1988:591–604. doi:10.2307/1445377

Sabaj Pérez M.H. (Ed.). 2013. Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an online reference. Version 4.0 (28 June 2013). Accessible at www.asih.org/resources/standard-symbolic-codes-institutional-resource-collections-herpetology-ichthyology. Accessed: 03 April 2014.

Schalk C.M. 2010. *Ceratophrys cranwelli* (Cranwell's Horned Frog) Diet. *Herpetological Review* 41:471.

Schalk C.M., Montaña C.G. 2011. *Ceratophrys cranwelli* (Cranwell's Horned Frog) Diet. *Herpetological Review* 42:409–410.

Scott N.J., Aquino A.L. 2005. It's a frog-eat-frog world in the Paraguayan Chaco: food habits, anatomy, and behavior of the frog-eating anurans. Pp. 243–259, in Donnelly M.A., Crother B.I., Guyer C., Wake M.H., White M.E. (Eds.), Ecology and Evolution in the Tropics: A Herpetological Perspective. University of Chicago Press, Chicago.

Seba A. 1734. Locupletissimi rerum naturalium thesauri accurata descriptio, et iconibus artificiosissimis expressio, per universam physices historiam. Opus, cui, in hoc rerum genere, nullum par exstitit. Ex toto terrarum orbe collegit, digessit, descripsit, et depingendum curavit. Tomus I. Apud J. Wetstenium, & Gul. Smith, & Janssonio-Waesbergios, Amstelaedami.

Shaw G. 1802. General Zoology or Systematic Natural History, Vol. 3. T. Davidson, London.

Silva N.R., Souza P.R., Gonçalves M.F., Demétrio M.F., Prado C.P. 2014. A voracious female during the courtship of *Ceratophrys cranwelli* (Anura: Ceratophryidae) in the Brazilian Chaco. *Herpetology Notes* 7:93–95.

Solé M., Marciano E. Jr., Dias I.R., Kwet A. 2010. Predation attempts on *Trachycephalus* cf. *mesophaeus* (Hylidae) by *Leptophis ahaetulla* (Colubridae) and *Ceratophrys aurita* (Ceratophryidae). Salamandra 46:101–103.

Sugai J.L.M.M, Faggioni G.P., Piatti L., Lemos A.A., Souza F.L., de Almeida Prado C.P. 2013. *Lepidobatrachus asper* Budgett, 1899 (Amphibia: Anura: Ceratophryidae): New country record, distribution map and natural history notes. *Check List* 9:133–135.

Targino M., Wild E.R. 2009. Amphibia, Anura, Microhylidae, *Hyophryne histrio:* distribution extension. *Check List* 5:24–26.

Tosi J.A. Jr. 1960. Zonas de vida natural en el Perú. *Boletin Tecnico Instituto Interamericano de Ciencias Agricolas de la OEA, Zona Andina* 5:1–271.

Vellard J. 1948. Batracios del Chaco Argentino. *Acta Zoologica Lilloana* 5:137–174.

Vera Candioti M.F. 2005. Morphology and feeding in tadpoles of *Ceratophrys cranwelli* (Anura: Leptodactylidae). *Acta Zoologica* 86:1–11. doi:10.1111/j.0001-7272.2005.00178.x

Vera Candioti M.F. 2007. Anatomy of anuran tadpoles from lentic water bodies: systematic relevance and correlation with feeding habits. *Zootaxa* 1600:1–175.

Wassersug R.J. 1971. On the comparative palatability of some dry-season tadpoles from Costa Rica. *American Midland Naturalist* 86:101–209. doi:10.2307/2423690

Wassersug R.J., Heyer W.R. 1988. A survey of internal oral features of leptodactyloid larvae (Amphibia: Anura). *Smithsonian Contributions to Zoology* 457:1–99. doi:10.5479/si.00810282.457

Werner E.E., Gilliam J.F. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* 15:393–425. doi:10.1146/annurev.es.15.110184.002141

Wilbur H.M. 1980. Complex life cycles. *Annual Review of Ecology and Systematics* 11:67–93.

Wild E.R. 1997a. Description of the adult skeleton and developmental osteology of the hyperossified horned frog, *Ceratophrys cornuta* (Anura: Leptodactylidae). *Journal of Morphology* 232:169–206. doi:10.1002/(SICI)1097-4687(199705)232:2<169::AID-JMOR4>3.0.CO;2-5

Wild E.R. 1997b. The Ontogeny and Phylogeny of Ceratophryine Frogs (Anura: Leptodactylidae). Ph.D. Dissertation, University of Kansas, USA.

Wild E.R. 1999. Description of the chondrocranium and osteogenesis of the chacoan burrowing frog, *Chacophrys pierotti* (Anura: Leptodactylidae). *Journal of Morphology* 242:229–246. doi:10.1002/(SICI)1097-4687(199912)242:3<229::AID-JMOR3>3.0.CO;2-N

Wild E.R. 2001. *Ceratophrys cranwelli* Predation. *Herpetological Review* 32:102.

APPENDIX. SPECIMENS EXAMINED

Specimens examined are from Museu Nacional Rio de Janeiro (MNRJ) and the University of Kansas Natural History Museum and Biodiversity Institute (KU). Institution abbreviations follow Sabaj Pérez (2013).

Ceratophrys aurita (*n* = 3): BRAZIL: **Bahia:** Nova Viçosa: MNRJ 19030–19031; **Espírito Santo:** Sooretema: Linhares, KU 92740.

Ceratophrys calcarata (*n* = 2): COLOMBIA: **Bolivar:** Alto de Quimari, 500 m: KU 144966; VENEZUELA: **Amazonas:** Puerto Ayacucho, 110 m: KU 207528;

Ceratophrys cranwelli (*n* = 2): BOLIVIA: **Santa Cruz:** Parapati: KU 92741; PARAGUAY: **Central:** Asuncion: KU 145088.

Ceratophrys ornata (*n* = 2): ARGENTINA: **Buenos Aires:** Olazabal, Tuzaingo: KU 175560; Necochea: KU 186864.

Chacophrys pierottii (*n* = 9): ARGENTINA: **Cordoba:** Totoralejos: KU 128846–51, 191927–28, 191932.

Lepidobatrachus asper (*n* = 2): ARGENTINA: **Santiago del Estero:** Santiago del Estero: KU 80782; PARAGUAY: **Central:** Asuncion: KU 145089.

Lepidobatrachus laevis (*n* = 1): ARGENTINA: **Formosa:** Formosa: KU 128853.