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Diet of juveniles and adults of the Cuban Giant Frog, *Eleutherodactylus zeus* (Anura: Eleutherodactylidae)

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Abstract

Anurans are gape-limited predators and therefore larger individuals are capable of consuming larger prey. Stomach contents of the Cuban Giant Frog, *Eleutherodactylus zeus*, from caves in the northeastern-most part of the Sierra de Quemados in Viñales National Park, Pinar del Río Province, Cuba, were indicative of ontogenetic changes in diet. Although niche overlap among size classes was relatively high, larger frogs consumed larger but fewer prey items. Predator and prey sizes were positively correlated in both adults and juveniles, whereas predator size and number of prey items per stomach was negatively correlated.

Keywords: Cuba, amphibians, caves, ontogenetic dietary shift.

Introduction

Anuran diets are affected by a series of extrinsic and intrinsic factors (Maneyro *et al*. 2004; Toledo *et al*. 2007) that include morphology (Biavati *et al*. 2004; Toledo *et al*. 2007; Pacheco *et al*. 2017), activity periods of predator and/or prey (Leivas *et al*. 2012a), individual social status (Pigliucci 2001; Bolnick *et al*. 2011), abundance (Bolnick *et al*. 2003), and temporal and seasonal variation in dietary resources (Miranda *et al*. 2006; Berazategui *et al*. 2007; Leivas *et al*. 2012a). Because frogs are gape-limited predators that ingest their prey whole, larger individuals are capable of consuming larger prey (Lima and Moreira 1993).

Although a number of studies have addressed ontogenetic dietary shifts in amphibians (Donnelly 1991; Lima and Moreira 1993; Hirai 2002; Biavati *et al*. 2004; Valderrama-Vernaza *et al*. 2009) and particularly in *Eleutherodactylus* frogs (Woolbright and Stewart 1987; Ovaska 1991; Whitfield and Donnelly 2006; Beard 2007; Olson 2011), only a few anecdotal accounts document the diets of juvenile *Eleutherodactylus* frogs in Cuba (i.e., *Eleutherodactylus riparius*; Valdés de la Osa and Ruíz García 1980).

The Cuban Giant Frog (*Eleutherodactylus zeus*) is endemic to the Cordillera de Guaniguanico in western Cuba, where it appears to rely on caves for reproduction (Alonso *et al*. 2015) and on forests for feeding (García-Padrón *et al*. 2021). Recently, García-Padrón *et al*. (2021) compared the diet of the Cuban Giant Frog associated with both caves and forest habitats during dry and wet seasons, noting that adults of this species are "sit-and-wait" predators with a diverse diet composed mainly of spiders, crickets, caterpillars, roaches, and snails. Herein, I present data on intraspecific dietary variation in this species, focusing on ontogenetic shifts in diet, in order to address three main questions. I examine (1) whether *E. zeus* exhibits variation in diet among age-classes (adults and juveniles), (2) what features, such as morphology and/or ethology, are responsible for the greatest variation in diets, and (3) what factors influence intraspecific overlap in diet (if it occurs) in the studied population.

Materials and Methods

This study was conducted in the northeastern-most part of the Sierra de Quemados in Viñales National Park, Viñales Municipality, Pinar del Río Province, Cuba (22.3242°N, 83.5037°W; WGS 84; elevation 250 m asl). During visits in July, August, September, and November 2018, and January and April 2019, I surveyed caves to depths of 50 m as well as 300 m into surrounding forests. Surveys were conducted at 2130–2330 h and limited to one night per site during each visit to avoid double counting the same individual. I measured snout–vent length (SVL) of all captured *E. zeus* (Fig. 1) with calipers to 0.01 mm and flushed each stomach in situ using methods of Solé *et al*. (2005) before releasing frogs at the site of capture. Stomach contents were stored in 20-ml vials with 70% ethanol until they were identified, counted, and measured (with a caliper) under a stereomicroscope to the lowest taxonomic level possible.

I recorded the number (N) and percentage (N%) of each type of prey, the frequency of occurrence (F, number of stomachs in which a given prey category was found) and the percentage (F%), and calculated Levins' index (B) (Krebs 1999) of trophic niche breadth: B = 1/∑Pi2; were Pi = fraction of items in the food category i. To standardize niche breadth (BA) (Hurlbert 1978), I divided B by the total number of resource states after correcting for a finite number of resources; range = 0 (no diversity, exclusive use of a single prey type, specialist) to 1 (highest diversity, prey items of all categories, generalist). I also calculated niche overlap between age-classes using Pianka's overlap index (POI) (Pianka 1973), which varies from 0 (no overlap) to 1 (complete overlap).

I used Mann-Whitney U-tests to compare prey types consumed by each age-class, Spearman correlation (r_S) tests to relate SVL and maximum prey size and number of prey per stomach, and linear regression to evaluate SVL with prey length and numbers of prey item consumed. Means are presented ± 1 SD (standard deviation).

Results

I captured 92 *Eleutherodactylus zeus*: 18 males (SVL = 65.5 ± 4.4 mm; 57.5–71.1 mm), 30 females (91.2 ± 12.9 mm; 65.5–114 mm), and 44 juveniles (26.9 ± 9.6 mm; 14.7–48.7 mm). Differences between age-classes were significant: males-females ($U = 8.000$, $Z = -4.553$, $p = 0.000$), males-juveniles ($U = 0.000$, $Z = -5.467$, $p = 0.000$), and females-juveniles ($U = 0.000$, $Z = -6.083$, $p = 0.000$).

Most *E. zeus* (76.1%) were observed with at least one prey item in the stomach (77.8% of males; 63.3% in females; and 84.1% of juveniles), whereas 23.9% had empty stomachs. Males consumed 1.93 prey/stomach ($N = 14$), females 1.74 prey/stomach ($N = 19$), and juveniles had 3.92 prey/stomach ($N = 37$).

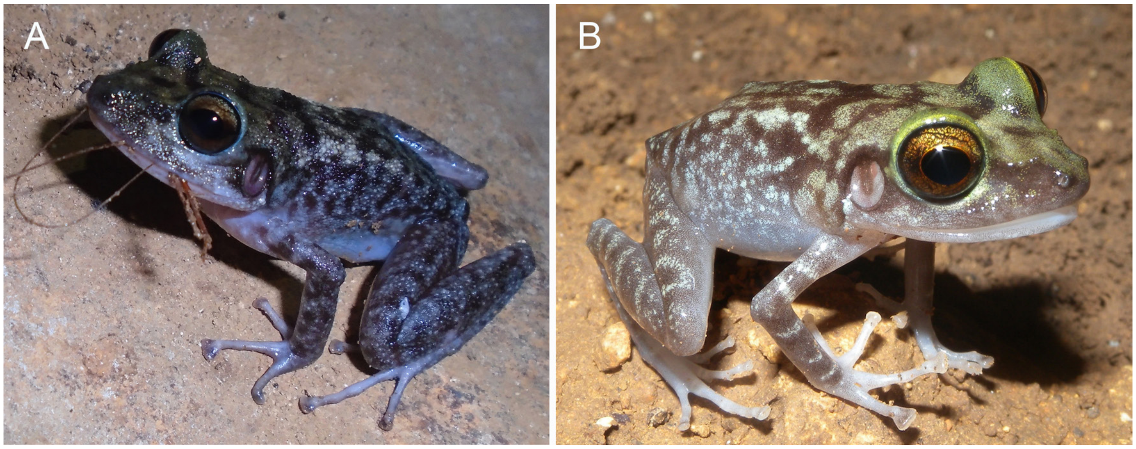

Figure 1. (**A**) Feeding male and (**B**) foraging juvenile Cuban Giant Frog (*Eleutherodactylus zeus*). Photos by the author.

Larger individuals consumed larger prey ($r_S = 0.674$; $R^2 = 0.294$; $p = 0.000$; $N = 70$) but a smaller number of items ($r_S = -0.462$; $R^2 = 0.1765$; $p = 0.000$; $N = 70$). Nonetheless, adults and juveniles consumed similar types of prey. Niche overlap in frequency of prey consumed was males/females (*POI* = 0.699), males/juveniles (*POI* = 0.586), and females/juveniles (*POI* = 0.450), and statistical differences were detected in the types of prey consumed between adults and juveniles ($U = 525.000$, $Z = -3.729$, $p = 0.000$). In general, juveniles consumed more spiders ($F_{\%} = 34.02$, $N_{\%} = 35.17$), ants ($F_{\%} = 9.28$, $N_{\%} = 8.97$), isopods ($F_{\%} = 8.25$, $N_{\%} = 13.10$), and snails ($F_{\%} = 7.22$, $N_{\%} = 5.52$) (Table 1; Fig. 2). Niche breadths decreased slightly with increasing size; juveniles had the greatest niche breadth ($B' = 0.36$) and those of males ($B' = 0.30$) and females were lower ($B' = 0.26$). No differences in types of prey consumed were detected among adults ($U = 405.000$, $Z = -0.779$, $p = 0.436$), which consumed mostly snails ($F_{\%} = 18.18$, $N_{\%} = 20.00$), crickets ($F_{\%} = 16.36$, $N_{\%} = 15.00$), roaches ($F_{\%} = 10.91$, $N_{\%} = 11.67$), and lepidopteran larvae ($F_{\%} = 10.91$, $N_{\%} = 11.67$) (Table 1; Fig. 2).

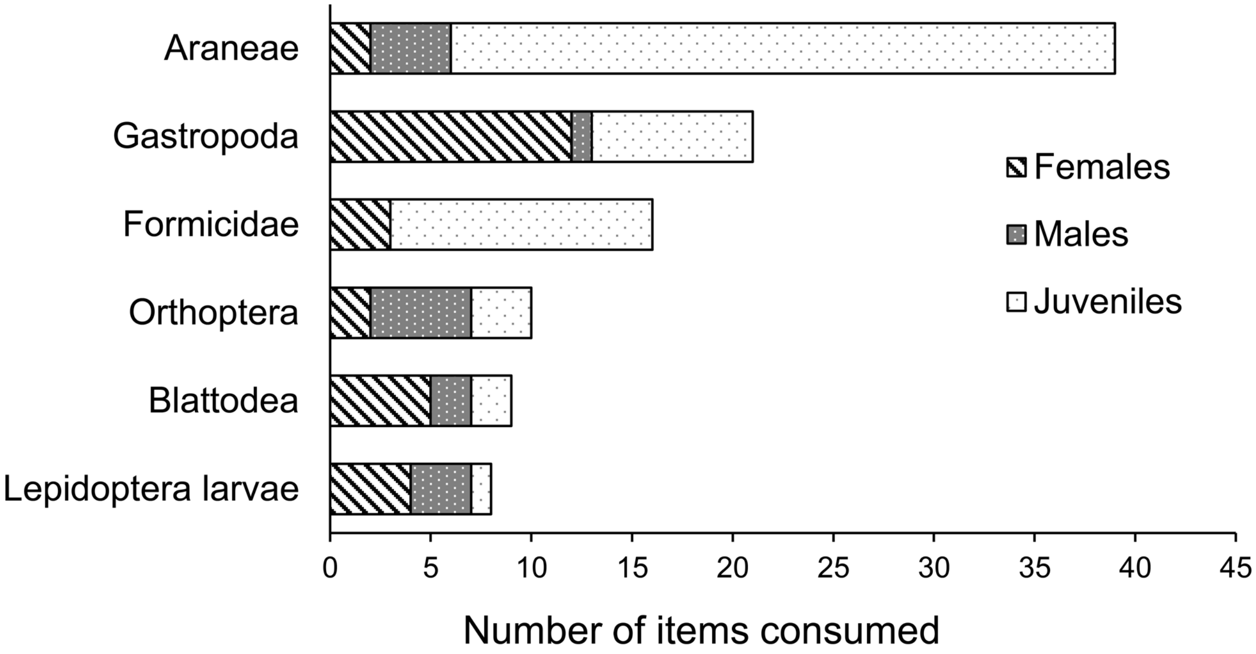

Figure 2. The six most frequently represented taxa in the diet of Cuban Giant Frog (*Eleutherodactylus zeus*).

Discussion

Because most studies of diets of Cuban frogs focused on adults (Valdés de la Osa and Zayas 1980; Alonso *et al*. 2001; García-Padrón and Borrego 2020; García-Padrón 2021; García-Padrón *et al*. 2021) or related only anecdotal observations (see Henderson and Powell 2009; García-Padrón and Borrego 2020; Rodríguez-Cabrera *et al.* 2020, for reviews), this study was the first to address a possible ontogenetic shift in the diet of a Cuban amphibian.

In anurans, variable age-based niche exploitation can be attributable to changes in size or developmental stages (Lima 1998; Lima and Magnusson 1998), and variation in the diets of males and females can result from differences in morphology (Shine *et al.* 2002) or energetic demands of reproduction (Belovsky 1978; Grayson *et al.* 2005; Martins *et al.* 2006; Wells 2007; Leivas *et al.* 2012b). For example, males expend a considerable amount of energy in vocalization and territorial defense (Giasson and Haddad 2006; Wells 2007; Leivas *et al.* 2012b), whereas the production and development of oocytes in females requires a substantial amount of energy (Wells 2007; Leivas *et al.* 2012a; Castro *et al.* 2013). In this study, despite the high overlap in the frequency of prey types consumed, I observed differences in the types, sizes, and numbers of prey consumed by adults and juveniles. Juveniles consumed a higher diversity of prey than adults. Those differences reflect juveniles taking greater numbers of smaller prey items (3.92 prey/stomach), whereas adults consumed lower numbers of larger prey items. Notably, however, spiders and snails were abundant in the stomach samples of all individuals regardless of age-class (Table 1; see also García-Padrón *et al.* 2021).

The consumption of *Anolis* lizards by Cuban amphibians has been recorded in only two isolated instances (García-Padrón *et al.* 2021; Hernández-Peraza and de Armas 2022), the former of which involved *E. zeus*. However, the discovery of another unidentified *Anolis* found in the stomach of a juvenile *E. zeus* (40.5 mm SVL) in this study suggests that *Anolis* lizards might not be all that rare in the diet of *E. zeus*—and possibly other larger species of frogs.

Individual specialization, a consequence of the niche expansion followed by competitive release, is achieved

Table 1. Prey of adults and juveniles of the Cuban Giant Frog (*Eleutherodactylus zeus*).

Class: Order	**Females (*N* = 19)**		**Males (*N* = 14)**		**Juveniles (*N* = 37)**		**TOTAL (*N* = 70)**	
	F (%)	**N (%)**	**F (%)**	**N (%)**	**F (%)**	**N (%)**	**F (%)**	**N (%)**
Diplopoda: Spirobolida	1 (3.45)	1 (3.03)	1 (3.85)	1 (3.70)	0	0	1 (0.66)	2 (0.98)
Chilopoda: Scolopendromorpha	0	0	1 (3.85)	1 (3.70)	1 (1.03)	1 (0.69)	2 (1.32)	2 (0.98)
Chilopoda: Scutigeromorpha	0	0	1 (3.85)	1 (3.70)	0	0	1 (0.66)	1 (0.49)
Arachnida: Amblypygi	0	0	1 (3.85)	1 (3.70)	1 (1.03)	1 (0.69)	2 (1.32)	2 (0.98)
Arachnida: Uropygi	0	0	1 (3.85)	1 (3.70)	0	0	1 (0.66)	1 (0.49)
Arachnida: Pseudoscorpiones	0	0	0	0	1 (1.03)	1 (0.69)	1 (0.66)	1 (0.49)
Arachnida: Araneae	2 (6.90)	2 (6.06)	4 (15.38)	4 (14.81)	23 (23.71)	39 (26.90)	29 (19.21)	45 (21.95)
Arachnida: Opiliones	0	0	1 (3.85)	1 (3.70)	5 (5.15)	7 (4.83)	6 (3.97)	8 (3.90)
Arachnida: Scorpiones	3 (10.34)	3 (9.09)	0	0	0	0	3 (1.99)	3 (1.46)
Arachnida: Acari	0	0	0	0	3 (3.09)	3 (2.07)	3 (1.99)	3 (1.46)
Entognatha: Protura	0	0	0	0	1 (1.03)	1 (0.69)	1 (0.66)	1 (0.49)
Entognatha: Collembola	0	0	0	0	5 (5.15)	16 (11.03)	5 (3.31)	16 (7.80)
Insecta: Orthoptera	3 (10.34)	3 (9.09)	6 (23.08)	6 (22.22)	2 (2.06)	2 (1.38)	11 (7.28)	11 (5.37)
Insecta: Hymenoptera	0	0	0	0	2 (2.06)	2 (1.38)	2 (1.32)	2 (0.98)
Insecta: Hymenoptera (Formicidae)	1 (3.45)	2 (6.06)	1 (3.85)	1 (3.70)	7 (7.22)	11 (7.59)	9 (5.96)	14 (6.83)
Insecta: Diptera	0	0	1 (3.85)	1 (3.70)	5 (5.15)	5 (3.45)	6 (3.97)	6 (2.93)
Insecta: Lepidoptera (larvae)	4 (13.79)	4 (12.12)	2 (7.69)	3 (11.11)	2 (2.06)	2 (1.38)	8 (5.30)	9 (4.39)
Insecta: Blattodea	4 (13.79)	5 (15.15)	2 (7.69)	2 (7.41)	3 (3.09)	3 (2.07)	9 (5.96)	10 (4.88)
Insecta: Coleoptera	2 (6.90)	2 (6.06)	0	0	2 (2.06)	4 (2.76)	4 (2.65)	6 (2.93)
Insecta: Coleoptera (larvae)	0	0	0	0	7 (7.22)	7 (4.83)	7 (4.64)	7 (3.41)
Insecta: Hemiptera	0	0	0	0	1 (1.03)	1 (0.69)	1 (0.66)	1 (0.49)
Insecta: Hemiptera (Heteroptera)	1 (3.45)	1 (3.03)	0	0	1 (1.03)	1 (0.69)	2 (1.32)	2 (0.98)
Insecta: Hemiptera (Cydnidae)	0	0	0	0	5 (5.15)	6 (4.14)	5 (3.31)	6 (2.93)
Insecta: Mantodea	0	0	0	0	1 (1.03)	1 (0.69)	1 (0.66)	1 (0.49)
Insecta: Zygentoma	0	0	1 (3.85)	1 (3.70)	0	0	1 (0.66)	1 (0.49)
Unidentified insects	0	0	0	0	2 (2.06)	2 (1.38)	2 (1.32)	2 (0.98)
Malacontraca: Isopoda	1 (3.45)	1 (3.03)	0	0	8 (8.25)	19 (13.10)	9 (5.96)	20 (9.76)
Gastropoda	7 (24.13)	9 (27.27)	3 (11.54)	3 (11.11)	7 (7.22)	8 (5.52)	17 (11.26)	20 (9.76)
Reptilia: Squamata	0	0	0	0	1 (1.03)	1 (0.69)	1 (0.66)	1 (0.49)
Inorganic material (paper fragment)	0	0	0	0	1 (1.03)	1 (0.69)	1 (0.66)	1 (0.49)

when individual variation increases rather than when individual niche width increases (Robinson *et al.* 1993). Trophic niche partitioning in *E. zeus* is related to two things. (1) Spatial partitioning: after laying eggs during reproduction, most adults leave the cave, and no parental care seems to occur (García-Padrón *et al*. 2021). (2) Food intake: predator/prey size in both adults and juveniles was positively correlated and predator size/number of prey per stomach was negatively correlated, suggesting that age-class competition for prey is likely to be minimal in at least this population of *E. zeus*.

During the present study, I noted that spiders, especially *Loxosceles* sp. and spiders of the families Lycosidae and Theraphosidae, were the most abundant prey inside a cave and its immediate surroundings. García-Padrón *et al.* (2021) suggested that the lower number of prey items observed in adult *E. zeus* inside caves was due to lower availability of suitable prey. Some studies (e.g., Prous *et al*. 2004; Tobin *et al.* 2013) supported this observation by pointing out that the diversity of arthropods in caves is lower than in forests. For *E. zeus*, prey size plays an important and determinant role: adults consumed fewer and larger prey, whereas juveniles effectively exploited small prey (e.g., spiders, isopods, springtails, and ants) (Table 1). On the other hand, although adults of both sexes took prey of similar lengths and the overlap index between sexes was high, males exhibited a slightly wider niche breadth and fed largely on spiders and crickets, whereas females consumed mostly snails, lepidopteran larvae, and roaches (García-Padrón *et al.* 2021; this study).

Most anurans are generalist predators, but they can distinguish between prey types (Solé *et al*. 2017), which allows different degrees of specialization (Freed 1982) and prey-capture strategies (Toft 1980). Most amphibians employ a "sit-and-wait" foraging strategy, whereas others are "active foragers," with some species using intermediate strategies (Caldart *et al.* 2012) and some even changing strategy depending on the availability of prey and/or the type of habitat they occupy (García-Padrón *et al.* 2022). Lima and Magnusson (2000) observed no ontogenetic changes in foraging activity Amazonian leaf-litter frogs. However, juvenile *Eleutherodactylus zeus* foraged more actively than adults (see García-Padrón *et al.* 2021) and consumed higher number of prey, features characteristic of "ant-specialist active predators" (see Toft 1980), whereas adults generally function as "non-ant specialist sit-and-wait" predators (García-Padrón *et al.* 2021). In this study, *E. zeus* fed largely on "sedentary prey" (those that move slowly and/or short distances such as snails, ants, diplopods, and caterpillars) (García-Padrón *et al.* 2020), supporting the contention that this species is a "sit-and-wait" predator throughout its life; however, "mobile prey" (e.g., roaches and crickets) also were consumed. This apparent versatility allows *E. zeus* to exploit a wide variety of prey categories when food is scarce, as in the dry season or in caves (García-Padrón *et al.* 2021) or when pressure attributable to competition for food resources is high among sympatric species of frogs of similar sizes (i.e., *Eleutherodactylus goini*, *E. klinikowskii*, and *Osteopilus septentrionalis*) (L.Y. García-Padrón, unpubl. data).

Human activities have affected the *E. zeus* population in the study area by destroying or modifying its habitats via factors including tourists visiting caves, clear cuts, and deposition of garbage in natural areas (Alonso *et al.* 2015; pers. observ.). García-Padrón and Borrego (2020) first recorded inorganic material consumed, presumably adventitiously, by *E. atkinsi* in the same area. Herein I found a juvenile (17.3 mm SVL) with a piece of toilet paper (approximately 27.4% of the individual´s size) in its stomach. Also, instances of piebaldism in *E. zeus* reported in adults and a juvenile (García-Padrón and Alonso 2019) might be associated with extrinsic factors, such as diet (Sage 1962), which in turn could be attributed to habitat alterations.

Fragile ecosystems, such as karstic regions, have scientific value because they provide shelter for endangered species and offer opportunities to study complex relationships (Alonso *et al.* 2015). Human-induced habitat alteration poses a risk to the survival of endemic and habitat-restricted species such as *E. zeus.* Policies must be developed and enforced to diminish negative human impact in natural areas, especially those that are close to human settlements or within the national park. Monitoring populations of endemic species, such as *E. zeus*, should be a part of any conservation plan in order to take timely action to ensure the survival of these species.

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