

Ontogenetic shifts in ambush-site selection of a sit-and-wait predator, the Chacoan Horned Frog (*Ceratophrys cranwelli*)

C.M. Schalk and L.A. Fitzgerald

Abstract: Ontogenetic shifts in habitat use are widespread among vertebrates. These niche shifts are often attributed to age-specific patterns of resource use, which are correlated with changes in morphology, diet, and habitat. We examined the ontogeny of ambush-site selection in a sit-and-wait predator, the Chacoan Horned Frog (*Ceratophrys cranwelli* Barrio, 1980), in the Gran Chaco ecoregion of Bolivia. We quantified covariation in microhabitat and morphological variables and tested for microhabitat selection against randomly selected points. We identified an ontogenetic shift in ambush-site selection between adult and metamorph frogs. When compared with random points, metamorphs selected a subset of available habitat, whereas adult frogs did not appear to select ambush sites. Metamorphs, compared with adults, selected ambush sites farther from a pond's edge with a greater proportion of dry mud. The metamorph of *C. cranwelli* may have selected ambush sites based on spatial distribution of certain size classes of prey. Alternatively, metamorphs could have selected sites to minimize asymmetric agonistic intraspecific interactions with adults. These mechanisms are not mutually exclusive and probably occur in concert. Habitat selection and ontogenetic niche shifts by these organisms provide insights to the trade-offs between foraging strategy and mortality risk.

Key words: amphibian, body size, tropical dry forest, foraging strategy, Gran Chaco, habitat selection, Neotropics.

Résumé : Les changements ontogéniques d'utilisation de l'habitat sont répandus chez les vertébrés. Ces changements de niche sont souvent attribués à des variations selon l'âge de l'utilisation des ressources, qui sont corrélées à des changements de morphologie, de régime alimentaire et d'habitat. Nous avons examiné l'ontogenèse de la sélection de sites d'embuscade chez un prédateur qui se tapit et attend, la grenouille cornue de Cramwell (*Ceratophrys cranwelli* Barrio, 1980), dans l'écorégion de Gran Chaco, en Bolivie. Nous avons quantifié la covariation de variables morphologiques et du microhabitat et vérifié s'il y avait sélection du microhabitat par rapport à des points choisis au hasard. Nous avons reconnu un changement ontogénétique dans la sélection du site d'embuscade entre les grenouilles adultes et en métamorphose. Comparées à des points choisis au hasard, les grenouilles en métamorphose choisissaient un sous-ensemble d'habitats disponibles, alors que les grenouilles adultes ne semblaient pas sélectionner leurs sites d'embuscade. Les grenouilles en métamorphose sélectionnaient des sites d'embuscade plus éloignés de la rive d'un étang et présentant une plus grande proportion de boue séchée que les grenouilles adultes. Il se peut que les *C. cranwelli* en métamorphose aient choisi des sites d'embuscade sur la base de la répartition spatiale de certaines classes de tailles des proies. Ou alors les individus en métamorphose sélectionnaient peut-être des sites qui minimisaient les interactions intraspécifiques agonistes asymétriques avec des adultes. Ces mécanismes ne sont pas mutuellement exclusifs et s'opèrent probablement en parallèle. La sélection de l'habitat et les changements ontogénétiques de niche par ces organismes jettent un éclairage sur les compromis entre la stratégie d'approvisionnement et le risque de mortalité. [Traduit par la Rédaction]

Mots-clés : amphibien, taille du corps, forêt tropicale aride, stratégie d'approvisionnement, Gran Chaco, sélection d'habitat, néotropiques.

Introduction

Body size is the single most important trait influencing energetics, life history, and ecology (Peters 1983; Schmidt-Nielsen 1984). Body size influences the breadth of resource utilization, which in turn affects species interactions and their response to the abiotic environment (Wilson 1975; Peters 1983; Werner and Gilliam 1984). Most animals undergo drastic changes in body size as free-living individuals during ontogeny. Because of the wide variation in body sizes of many animal species, the ecological niche of a single species is expected to vary for different body size classes, with multiple size classes occupying distinct ecological niches (Werner and Gilliam 1984; Mittelbach et al. 1988; Subalusky et al. 2009). Ontogenetic niche shifts are characterized by changes in morphology, resource use, and habitat that occur in concert (Werner and Gilliam 1984).

The most frequently studied aspects of ontogenetic niche shifts in vertebrates are relationships between size, diet, and habitat (Stamps 1983; Werner and Gilliam 1984; Winemiller 1989; Olson 1996; Byström et al. 2012). The selection of habitat sites by an individual is a product of many interacting factors, including morphological and physiological constraints. Patterns of habitat selection by individuals reflect access to resources (e.g., food), risks of competition and predation, and any number of ecophysiological factors (Eskew et al. 2009; Schalk et al. 2010). As body size increases during ontogeny, importance and strengths of these interacting factors shift, resulting in the ability of individuals to use different habitats and food resources. Because of the interaction between habitat and prey resources (i.e., different prey are available in different habitats), shifts in these aspects of the niche occur in concert. Documenting the patterns of ontogenetic shifts

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in habitat allow one to infer how size-specific selection pressures may drive patterns of resource use, as well understand the ecological roles of predators, competitors, and prey (Stamps 1983). In gape-constrained predators for example, change in size of gape during ontogeny affects the size and type of prey that can be consumed (Christian 1982; Woolbright and Stewart 1987; Winemiller 1989; Montaña et al. 2011).

The anuran life cycle has one of the most distinct and remarkable ontogenetic niche shifts in all vertebrates, where the aquatic larva metamorphoses into a carnivorous, terrestrial adult (Wilbur 1980). Many species of anurans undergo an increase in body size of several orders of magnitude as free-living frogs (Werner 1986) and it is expected that these organisms will experience significant variation in their ecological niche. Given that frogs can constitute a significant portion of the animal biomass in some ecosystems (Gibbons et al. 2006) and serve as both predators (Wells 2007) and prey (Toledo et al. 2007) at multiple age classes, understanding their patterns of resource use can have important implications for their population regulation, as well as community structure (Werner and Gilliam 1984; Werner and Hall 1988; Olson 1996). While the ontogenetic niche shift during metamorphosis has received considerable attention (Wilbur 1980; Werner 1986), there are surprisingly few studies of postmetamorphic ontogenetic niche shifts in anurans. There is some evidence documenting ontogenetic niche shifts in postmetamorphic anurans, especially in diet (Christian 1982; Woolbright and Stewart 1987; Lima 1998; Lima and Magnusson 1998; Hirai 2002), and less frequently, in habitat use (Freeland and Kerin 1991). The studies focused on diet have generally found that during ontogeny, anurans change in the type of prey consumed as well as their size, with larger individuals consuming larger prey (Hirai 2002; Lima and Magnusson 1998), which was attributed to the change in both habitat use and gape size, an important predictor in the prey a frog is able to consume (Emerson 1985). However, not all species of post-metamorphic anurans exhibited ontogenetic shifts; Lima and Magnusson (2000) only observed three of the six species of Amazonian leaf-litter frogs exhibiting an ontogenetic change in foraging activity. The ontogenetic shifts in habitat use of the Cane Toad (*Rhinella (Bufo) marina* (L., 1758)) have been attributed to the physiological constraints of the metamorphs; their smaller body size made them more susceptible to water loss and thus they were often encountered close to the edge of the breeding pond (Freeland and Kerin 1991). In this study, we sought to explore the ontogenetic niche shift in habitat selection, specifically of ambush sites, in a sit-and-wait predator, the Chacoan Horned Frog (*Ceratophrys cranwelli* Barrio, 1980). Frogs of the genus *Ceratophrys* Wied-Neuwied, 1824 are characterized by a very large gape, an extreme sit-and-wait foraging mode, and cryptic behavior (Schalk et al. 2014). They are well-known opportunistic predators that consume a variety of invertebrate and vertebrate prey (Schalk et al. 2014). As this species undergoes a nearly fourfold increase in body size during ontogeny of the postmetamorphic life stage, we predicted adult and metamorph frogs would differ in their general patterns of ambush site. We also predicted adult and metamorph frogs would select ambush sites in nonrandom fashion, based on identifiable habitat characteristics.

Materials and methods

Study species and study site

Ceratophrys cranwelli is a relatively large frog endemic to the Gran Chaco ecoregion of Argentina, Bolivia, Brazil, and Paraguay (Cei 1980). Like other species of ceratophryids, *C. cranwelli* possesses a gape width >50% of their body length. Both metamorphs and adults of this species are thus capable of consuming large prey in relation to their body size, and relatively larger prey compared with other anurans (Scott and Aquino 2005; Schalk 2010; Schalk et al. 2014).

The Bolivian Gran Chaco, located in southeastern Bolivia, contains large expanses of semiarid thorn forest (Navarro and Maldonado 2002). Rainfall in the region of our study site (mean rainfall = 513 mm) is seasonal, occurring between November and March (Navarro and Maldonado 2002). Our study site was located in the Isoceño community of Yapiroa (19.60721°S, 62.57492°W), 1 of approximately 25 indigenous communities distributed along the Parapetí River in the indigenous territory of Isoso.

Frog surveys

We conducted nightly surveys for *C. cranwelli* from 8 to 29 March 2009 and from 22 to 25 April 2009 ($n = 26$ nights). Each night, we canvassed the area around and between 15 breeding ponds (ephemeral: $n = 14$; semipermanent: $n = 1$) from the hours of 2000 until 0000. The distance between ponds was 50–400 m and ponds ranged in size from 40 to >1000 m². We randomized the order of the ponds surveyed each night. We assumed all frogs encountered were in the ambush position, as we never encountered any individuals that were moving, calling males, or amplexant pairs.

When a frog was encountered, we estimated microhabitat variables in a 0.25 m² quadrat, divided into 25 equal 0.01 m² squares, centered on the frog's location. At the same time (within minutes), we also measured the same variables at a randomly chosen, paired, unoccupied site. This paired approach allowed us to test for microhabitat selection among individuals at the appropriate scale of observation (Beck and Jennings 2003; Fitzgerald and Nelson 2011). At occupied and random sites, we measured percent cover of plants, woody debris, water, wet mud, and dry mud. We defined wet mud as being malleable when pressure was exerted on the surface, whereas dry mud was not. We also recorded the distance to nearest suitable cover (e.g., logs or plants), distance to the pond edge, and depth of the water to the nearest centimetre. We classified encounters according to whether the frog or random site was within or outside the pond. A frog was assigned a negative value when it was found within a pond and a positive value when it was encountered outside the pond.

A random point could fall anywhere along the cardinal directions from 0.25 to 2 m from the occupied site. The cardinal direction was chosen at random and the distance from the occupied site was chosen with a random number generator (the @Rand function in Microsoft Excel™). There was an equal chance the random points could be closer to or farther from the pond edge with respect to the site occupied by that specific frog. The random points occurred in a space that could have been selected by that frog, at the time of observation, and was a sample of a site the individual could have selected but did not at that moment in time and space. No mean difference between occupied and random variables would mean no habitat selection. This method is informative because it focuses on individual microhabitat selection. In contrast, randomly selecting a sample of points in the study area would bias the data set towards places that were out of the realm of feasible choices for the individuals that we observed. Our approach allows us to match comparisons of occupied and random sites with the scale of microhabitat selection of the individuals.

We measured snout-vent length (SVL) (to the nearest millimetre using dial calipers) of each frog captured. To identify shifts in microhabitat selection that indicate an ontogenetic shift, we calculated the running mean of the frog's SVL against the values of the habitat variables using a lag of three. Frogs were marked by toe clipping and immediately released, except a subset ($n = 15$) that was collected and deposited in the Herpetology Collection in Museo de Historia Natural, Noel Kempff Mercado, in Santa Cruz de la Sierra, Bolivia.

Statistical analyses

Using museum specimens, we analyzed allometry of gape width by log-transforming the data and regressing gape width to SVL. Habitat data were not normally distributed and standard

transformations failed to normalize distributions and homogenize group variances. Therefore, we used nonparametric univariate and multivariate statistics to analyze patterns of habitat selection. We tested for differences in habitat variables for adult and metamorph frogs, without inclusion of the random points, using a Mann–Whitney U test. To test for ambush-site selection in adults and metamorphs, we performed Wilcoxon paired-sample tests on microhabitat variables for ambush sites and nearby paired random sites. To test for multivariate microhabitat selection, we conducted a one-way analysis of similarity (ANOSIM; Bray–Curtis distance; permutations = 9999) on occupied and random sites for adults and metamorphs, ANOSIM is a nonparametric alternative to MANOVA that does not depend on multivariate normality of the data (Gotelli and Ellison 2004). ANOSIM produces the statistic R , which indicates the magnitude of the difference among groups. An $R = 1.0$ indicates that assemblages are completely different, while an $R = 0.0$ would reflect complete similarity (Clarke and Warwick 1994). Analyses were conducted in the program PAST (Hammer et al. 2001). To further evaluate patterns of habitat selection, we calculated nonmetric multidimensional scaling (NMDS) analyses of all frogs combined and for adults and metamorphs separately. The NMDS ordination was constructed using presence–absence data by location of adult and metamorphs, adults and their respective random points, and metamorphs and their respective random points. NMDS is well suited for our purpose because it is unconstrained by environmental variables (McCune and Grace 2002). We could then fit environmental variables to the ordination as vectors and identify important environmental gradients. The ordination was completed using the Bray–Curtis distance measure in PC-ORD (McCune and Mefford 1999). In NMDS, the robustness of the ordination is indicated by its stress value: <0.2 gives a potentially useful two-dimensional picture, <0.1 corresponds to a good ordination, and <0.05 is an excellent representation (Clarke and Warwick 1994).

Results

We captured 96 individuals and none were recaptures. The running means of distance to pond's edge and proportion of dry mud shifted distinctly at 42 mm SVL (Figs. 1A, 1B). Frogs smaller than 42 mm SVL were found in a wide range of distances to pond's edge, with a preponderance of small individuals relatively far from the edge, and on dry mud.

These results gave us an ecological basis for classifying the frogs as metamorphs (<43 mm SVL) and adults (>42 mm SVL). The 42 mm size break is also consistent with the upper SVL of first-year metamorphs in *C. cranwelli* (generally between 25 and 42 mm) (Fabrezi 2011; C.M. Schalk, personal observation) and adults (those frogs with an SVL greater than the range of SVL values of metamorphs) (Fig. 2). Gape width of *C. cranwelli* was significantly correlated with SVL and exhibited a slightly negative pattern of allometric growth in relation to SVL ($y = -0.13747 + 0.95362x$, $p < 0.001$). We only found *C. cranwelli* near ephemeral ponds; no individuals were found around the semipermanent pond or between ponds. The NMDS axes 1 and 2 accounted for 72% of the variation (axis 1: 57.1%; axis 2: 14.9%) and had a stress value of 0.12, indicating the ordination was informative (Fig. 3A). ANOSIM revealed that adults and metamorphs of *C. cranwelli* occupied different microhabitats (Fig. 3A; $R = 0.1842$, $p = 0.0029$). Metamorphs occurred significantly farther from the pond's edge (Mann–Whitney U test, $U = 592$, $p = 0.01086$) and occupied areas with a higher proportion of dry mud compared with adults (Mann–Whitney U test, $U = 571.5$, $p = 0.001698$), whereas adults were found in sites with a higher proportion of water (Mann–Whitney U test, $U = 550.5$, $p = 0.0003371$) and in deeper water (Mann–Whitney U test, $U = 655.5$, $p = 0.00029$).

Fig. 1. Running mean of (A) snout–vent length (SVL) of Chacoan Horned Frogs (*Ceratophrys cranwelli*) versus distance from the pond's edge and (B) SVL of *C. cranwelli* versus percent cover of dry mud.

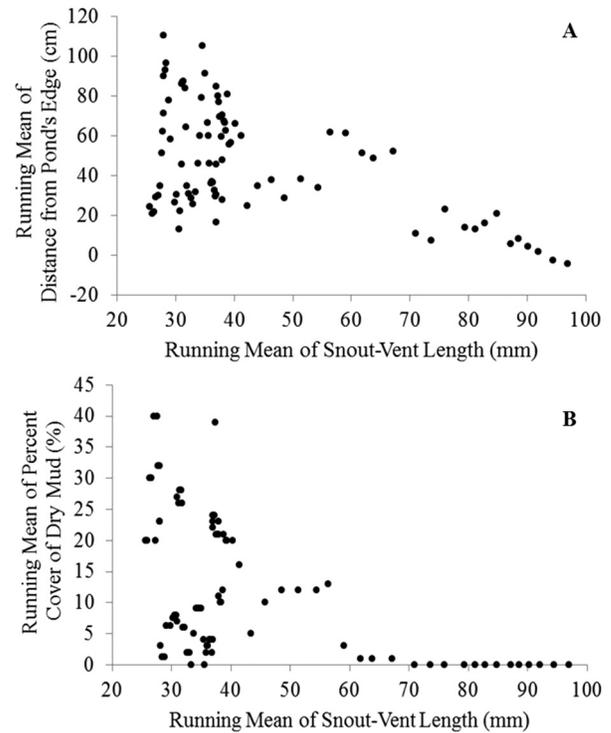
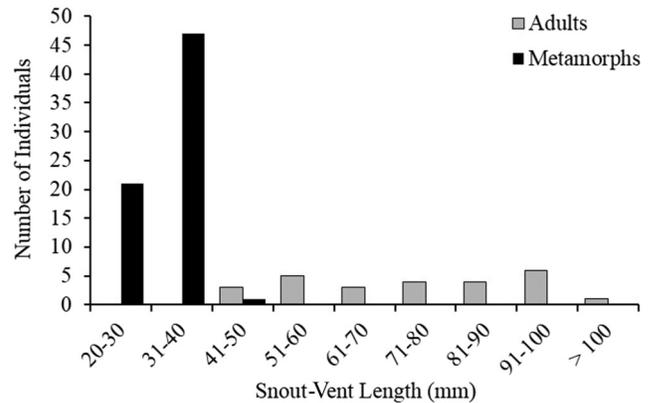


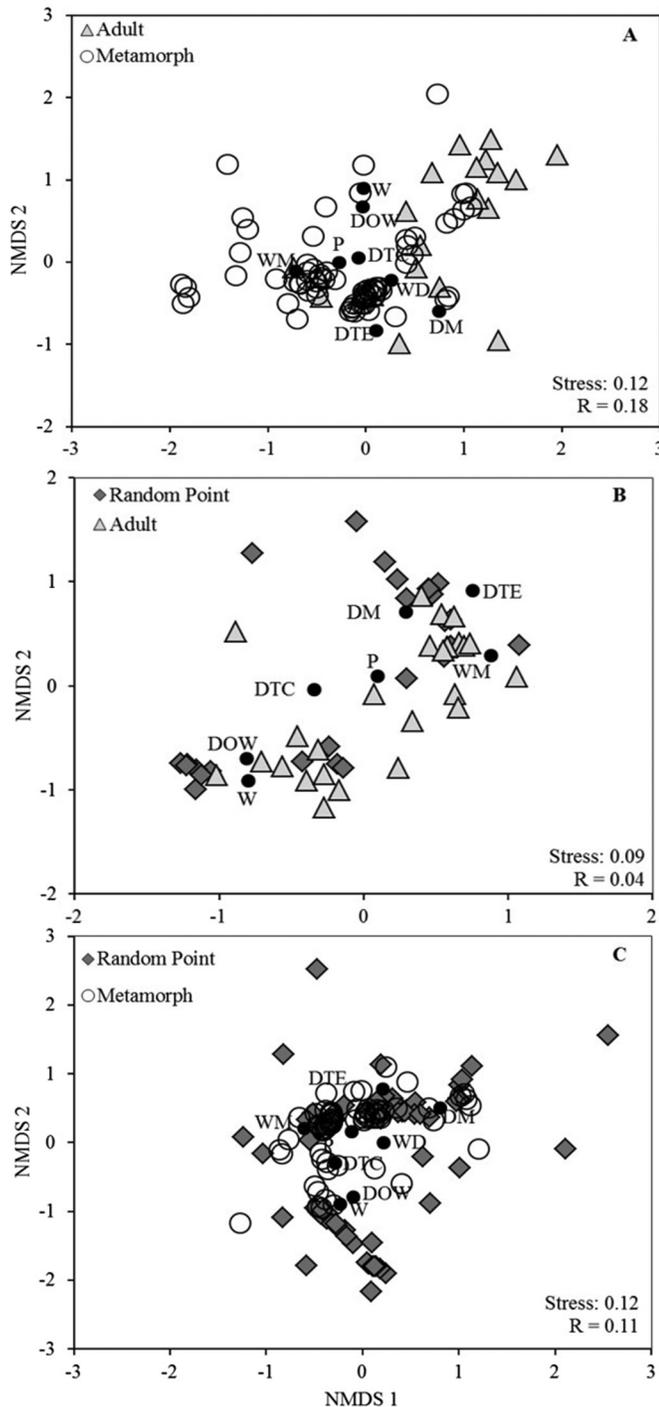
Fig. 2. Size-class distribution of the metamorph and adult Chacoan Horned Frogs (*Ceratophrys cranwelli*).



The NMDS ordination of *C. cranwelli* adults and their respective random points resulted in two axes accounting for 68.6% (axis 1: 56.6%; axis 2: 12.0%) of the variation, with the ordination considered to be good with its stress value of 0.09 (Fig. 3B). Adults generally exhibited no selection in their ambush sites when compared with their respective random points (Fig. 3B; ANOSIM, $R = 0.03729$, $p = 0.1005$). The Wilcoxon paired-sample tests revealed the percentage of dry mud was the only microhabitat variable that was significantly different between adults and random points ($z = 2.218$, $p = 0.03$); adults avoided areas with a higher proportion of dry mud when compared with their random points.

The NMDS ordination of the *C. cranwelli* metamorphs and their respective random points resulted in two axes accounting for 61.2% (axis 1: 46.6%; axis 2: 14.6%) of the variation, with the ordination considered to be useful with its stress value of 0.12 (Fig. 3C). Metamorphs selected a smaller proportion of the available habitat

Fig. 3. Nonmetric multidimensional scaling (NMDS) ordination of the Chacoan Horned Frog (*Ceratophrys cranwelli*) (A) metamorphs and adults, (B) adults and their respective random points, and (C) metamorphs and their respective random points in relation to the environmental variables (black circles) measured. Environmental variables are as follows: DTE, distance to edge of pond; DTC, distance to cover; WM, percent cover of wet mud; DM, percent cover of dry mud; W, percent cover of water; P, percent cover of plants; WD, percent cover of woody debris; DOW, depth of water. The *R* value is the *R* statistic produced from the analysis of similarity (ANOSIM).



to use as ambush sites (Fig. 3C; ANOSIM, $R = 0.1051$, $p = 0.0001$). Wilcoxon paired-sample tests revealed metamorphs selected points significantly farther from water than the random points ($z = 2.382$, $p = 0.017219$). Metamorphs selected areas with a significantly higher proportion of dry mud ($z = 4.697$, $p < 0.0001$) and occurred significantly less in areas with a higher percentage of water cover ($z = 3.147$, $p = 0.003$) and water depth ($z = 4.365$, $p < 0.0001$).

Discussion

Selection of foraging sites is the product of a trade-off driven by food availability and the cost, or perceived cost, concomitant with those sites (Werner et al. 1983; Lima and Dill 1990; Schalk et al. 2010; Eskew et al. 2009). In this study, we observed an ontogenetic niche shift in the form of ambush-site selection, between metamorphs and adults of *C. cranwelli*. At the broader habitat scale, we observed a pattern where both niche classes of *C. cranwelli* were associated with ponds. Duellman and Lizana (1994) studied the ecology of a congener, the Amazonian Horned Frog (*Ceratophrys cornuta* (L., 1758)), in the Peruvian Amazon and they did not observe ontogenetic shifts in habitat selection in that species; they also observed that *C. cornuta* used different types of habitat compared with those used by *C. cranwelli* in this study. Individuals of *C. cornuta* were found more often in the leaf litter of the surrounding forest and few individuals were found within the vicinity of water, the majority of which were calling males (Duellman and Lizana 1994). Members of the genus *Ceratophrys* are sit-and-wait predators and rely on prey that possess a higher mobility than themselves to increase encounter rates (Huey and Pianka 1981; Taigen and Pough 1983). Additional attributes of prey of sit-and-wait predators include being fewer in number, more solitary, and relatively large in size (Toft 1980). Suitable prey for *C. cornuta* are likely more dispersed and widespread in wet tropical rain forests, which may account for the observed distribution of *C. cornuta* across the entire forest (Duellman and Lizana 1994). In contrast, the xeric nature of the habitat of the Gran Chaco may cause prey to be concentrated around ponds, which may account for the observed ambush-site selection in *C. cranwelli*. While this region does have a pronounced rainy and dry season as most areas in the tropics, this area of the Chaco receives the least amount of rainfall across the entire ecoregion, with corresponding high variation in precipitation (Navarro and Maldonado 2002). It typically may not rain for up to 2 weeks even during the rainy season (C.M. Schalk, personal observation). Thus, breeding and foraging habitat for *C. cranwelli* is patchy across the dry Chaco landscape. The prey of *C. cranwelli* may be concentrated around these breeding ponds and likely drive the aggregation of *C. cranwelli* that we observed.

The morphological constraints of a size class also affect the types of food available that can be used by an individual in a foraging site (Werner and Gilliam 1984). Studies of trophic ontogeny of anurans have revealed that prey size increases with increasing gape width (Christian 1982; Hirai 2002), though there have been exceptions (Lima 1998). Skull size is an important predictor in the size and type of prey a frog can consume, with those species possessing a wide gape (e.g., *Ceratophrys* spp.) being adapted for consuming large prey such as vertebrates (Emerson 1985). Although data on prey type, size, and number were unavailable for this study, the allometric analysis of gape width provides insights into foraging differences of the two ontogenetic niche size classes. As SVL increased, gape width increased linearly and rapidly with SVL, increasing over fivefold during ontogeny. Allometry of gape width was slightly negative (slope = 0.953), with small metamorphs possessing relatively large gape widths. Thus, both small and large individuals possess the morphology to consume large prey, but during ontogeny, larger individuals are able to consume increasingly larger prey. This species has been observed preying upon vertebrates at both the metamorph and the adult life stages

(Schalk et al. 2014). Organisms that are gape-limited and that undergo a large increase in body size during ontogeny often exhibit a size-dependent shift in diet (Christian 1982; Werner and Gilliam 1984; Byström et al. 2012); prey availability is a factor responsible for the observed ontogenetic niche shift. Because there is large difference in the size of the prey that can be consumed between adults and metamorphs, it is unlikely that the metamorph size class would be using similar food resources as the adults.

Selection of foraging sites coincides with high availability of food (Harris 1986; McCormick 1998). The ambush-site selection of the adults and metamorphs may be reflective of the spatial and size segregations of the prey of *C. cranwelli*, which includes other species of frogs (Scott and Aquino 2005; Schalk et al. 2014). Ponds in the dry Chaco serve as breeding sites for 17 species of anurans found in our study site (C.M. Schalk and L.A. Fitzgerald, unpublished data); individuals of many species are concentrated around the pond's edge to call, oviposit, or as they emerge from the pond as metamorphs. When compared with the metamorphs, adults of *C. cranwelli* used ambush sites closer to the pond's edge; when compared with their random points, adults of *C. cranwelli* avoided areas with a high proportion of dry mud. Ambush sites near the pond's edge would increase encounter rates with frog prey (Scott and Aquino 2005; Schalk and Montaña 2011), which coincides with the observations of Schalk et al. (2014) that documented a high proportion of frog prey in the diet of *C. cranwelli*. However, the sites of the adult frogs were no different from the random sites, which were within 2 m of the ambush site. Adults of *C. cranwelli* may be able to use a relatively broad range of ambush sites close to the pond's edge, which is why our site-selection analysis did not distinguish random sites from the ambush sites for adults. Conversely, the ambush sites selected by metamorphs were significantly different than the random sites. *Ceratophrys cranwelli* metamorphs are more limited in the range of the size of prey that they can consume and the distribution of smaller prey items consumed by metamorphs may exert a stronger influence on the ambush sites that they select. It has been well documented that juvenile amphibians constitute the dispersal stage for many pond-breeding amphibians (Semlitsch 2010). Metamorphs of *C. cranwelli* have been observed consuming metamorphs of other anuran species (Schalk 2010; Schalk et al. 2014) and their selection of sites farther from the pond's edge may be in response to encounter rates with small, emerging metamorphs of other frog species that may be dispersing into the terrestrial landscape and other small prey such as terrestrial invertebrates.

Counteracting the ability of an animal's foraging strategy are the mortality risks associated with that habitat (Lima and Dill 1990). *Ceratophrys cranwelli* metamorphs selected a smaller subset of the total available habitat, specifically sites that were farther from the pond's edge and with a higher proportion of dry mud, whereas the ambush sites used by the adults were no different from the random sites. Smaller body sizes are more susceptible to desiccation because of a higher surface area to volume ratio and these physiological constraints can influence the spatial distribution of an organism (Freeland and Kerin 1991; Eskew et al. 2009). In anurans, metamorphs tend to be associated with more mesic microhabitats because they are more vulnerable to desiccation (Freeland and Kerin 1991), yet we observed an opposite pattern in our study. The physiological cost may be low for metamorphs because they are adapted to the arid habitat of the Gran Chaco (e.g., the ability to form cocoons to limit water loss while aestivating; Cei 1980), thereby allowing them to select and exploit foraging sites that could be unavailable to other anuran species that may be more constrained by their physiology (Freeland and Kerin 1991).

Various forms of intraspecific interactions (e.g., cannibalism, competition for space, avoidance behaviors) between adults and metamorphs could each drive the pattern of microhabitat selection that we observed. Displacement interactions between adults

and metamorphs is possible, but seems unlikely to be driving the observed pattern. Metamorphs could be at risk of cannibalism by adults near the pond's edge, as an increase in the difference in body size increases the potential for asymmetric predatory interactions (Werner et al. 1995). However, cannibalism has not been observed in the postmetamorphic life stage of this species (Schalk et al. 2014), and while cannibalism is assumed to occur frequently in the frogs of the family Ceratophryidae, this overgeneralization appears to stem from very limited data (Schalk et al. 2014). Some species of anurans shift in their foraging strategy during ontogeny (Lima 1998), but *C. cranwelli* maintains its sit-and-wait strategy as both metamorphs and adults. Given that species' with this foraging strategy relies on large, mobile, prey (Toft 1980), adult and metamorph of *C. cranwelli* may have a low likelihood of encountering one another, as they are both sit-and-wait predators. Thus, metamorphs may select sites that have a low likelihood of encounter rates with adults to minimize any potential for cannibalistic interactions, as we observed a disparity in the ambush sites selected among the two different size classes. The mechanism driving this pattern could be an evolutionary relict, i.e., "ghost of cannibalism past" (sensu Connell 1980), where cannibalism could have driven microhabitat selection; however, cannibalism is now rare. The alternative hypotheses that microhabitat differences are due to avoidance interactions or driven by distribution of prey sizes in different microhabitats are not mutually exclusive and both may be influencing the ontogenetic shift that we observed. We did not measure distribution and abundance of prey during our study and further research would be needed to disentangle the roles of avoidance and prey-based habitat selection in these frogs.

It is unlikely that territoriality explains the differences in ambush-site selection between adults and metamorphs of *C. cranwelli*. Territorial behavior, for example, allows for access to critical resources (Kaufmann 1983), but the primary purpose of territoriality in anurans is associated with reproduction (Wells 1977; Pröhl 2005). We did not observe any reproductive behavior (e.g., calling males or pairs in amplexus) during our study that would indicate the establishment of territories by the adults. Females of *C. cranwelli* exhibit aggressive behaviors during courtship and when in amplexus, but it is unknown whether the purpose of such behaviors are due to female mate choice or a type of predatory behavior (Schalk and Montaña 2011; Schalk et al. 2014; Silva et al. 2014).

Our study adds to the scant literature on ontogenetic shifts in the postmetamorphic life stage of anurans and provides the first information on ontogenetic differences in habitat selection in this species. Intraspecific and interspecific variations in body size influences the type and strength of the ecological interactions (Werner and Gilliam 1984). Habitat selection is the most fundamental and important aspect in understanding a species' niche (Pianka 2000; Morris 2003; Wells 2007), but it is acknowledged that habitat selection may change during ontogeny (Werner and Gilliam 1984). The pattern that arises from studying ontogenetic shifts in habitat selection provides an important foundation to generate and test mechanistic hypotheses to elucidate the ecological factors driving the observed pattern (Werner 1998). Combining this information with diet, activity patterns, and prey distribution may allow one to make better predictions regarding the mechanisms driving the observed niche shifts in postmetamorphic anurans, and be better able to accurately describe and understand the factors influencing their community structure.

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