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POPULATION STATUS AND NATURAL HISTORY NOTES ON THE CRITICALLY ENDANGERED STREAM-DWELLING FROG *CRAUGASTOR RANOIDES* (CRAUGASTORIDAE) IN A COSTA RICAN TROPICAL DRY FOREST

HÉCTOR ZUMBADO-ULATE[1,2], FEDERICO BOLAÑOS[1], BEATRIZ WILLINK[1], FERNANDO SOLEY-GUARDIA[3]

[1]*Escuela de Biología, Universidad de Costa Rica. San Pedro, San José, Costa Rica, e-mail: hugozu1@yahoo.com*
[2]*Asociación para la Conservación y el Estudio de la Biodiversidad, San Pedro, Costa Rica*
[3]*Department of Biological Sciences, Macquarie University, Sydney, New South Wales 210, Australia*

***Abstract.*—The *Craugastor rugulosus* species series has been one of the most affected clades by the decline of amphibian populations in Mesoamerica. These stream-dwelling frogs are threatened at all altitudinal ranges throughout their distribution. *Craugastor ranoides* is categorized as Critically Endangered on the IUCN Red List due to the disappearance of populations in the highlands and lowlands of Costa Rica. Currently the species is only found on the Santa Elena Peninsula. Additional ecological and natural history studies are necessary to formulate conservation plans for this species, which should include captive breeding programs and continuous monitoring of wild populations. We conducted a study of density, habitat use, and morphometrics of *C. ranoides* in three streams on the Santa Elena Peninsula Guanacaste, Costa Rica, during two consecutive dry seasons. The density of adult frogs and the probabilities of detection were similar during both dry seasons but we found differences in both parameters between streams. Counts of juveniles and subadults differed between seasons and between streams. Stream sector (50-m length) occupancy was approximately 80% during both dry seasons. We found most frogs motionless on boulders, but juveniles also frequented leaf litter. Sexual dimorphism was found in snout-vent length, mass, and tympanum diameter in subadults and adults. This study establishes a baseline for further monitoring of wild populations. Additional research and monitoring are necessary to detect possible changes in abundance and potential decline of these populations, which might be the only ones remaining in Costa Rica.**

Key Words.—amphibian declines*; Craugastor ranoides*; *Craugastor rugulosus* group; endangered species; tropical dry forest

INTRODUCTION

Approximately 33% of the populations of existing species of amphibians have declined and are currently under threat, and many other species have become extinct (Stuart et al. 2004). Numerous cases of population declines and extinctions have occurred in undisturbed sites and protected pristine habitats worldwide (Crump et al. 1992; Fellers and Drost 1993; Lips 1998). Such declines have been associated with various factors, including disease and global climate change (Young et al. 2001). Fortunately, in the last few years some supposedly extinct species reappeared in several regions of the world (e.g., Retallick et al. 2004; La Marca et al. 2005) including Costa Rica, where populations of the following presumably extinct species have been reported: *Isthmohyla angustilineata* (Hylidae; Nishida 2006), *Atelopus varius* (Bufonidae; Rainmaker Conservation Project. 2007. Harlequin Toad. Available from http:// www.rainmakercostarica.org [Accessed 10 May 2011]), *Incilius holdridgei* (Bufonidae; Abarca et al. 2010), *Duellmanohyla uranochroa* and *Isthmohyla rivularis* (Hylidae), *Lithobates vibicarius* (Ranidae), *Silverstoneia nubicola* (Dendrobatidae; Bolaños 2009) and *Craugastor fleischmanni* (Craugastoridae; Ryan, M.J., F. Bolaños, and G. Chaves. 2011. Museums help prioritize conservation goals. Available from http:// www.sciencemag.org/content/329/5997/1272/reply#sci_ el_13658 [Accessed 10 May 2011]). The dramatic decline of amphibian populations, along with the rediscovery of species presumed to be extinct, emphasizes the necessity to prioritize field monitoring of declining species to gain a better understanding of their population dynamics (Abarca et al. 2010).

In Central America, most declines have occurred at intermediate elevations (Bolaños and Ehmcke 1996; Lips 1998; Pounds et al. 1997, 1999; Puschendorf et al. 2006a), including the extinction in Costa Rica of the Golden Toad *Incilius periglenes* (Pounds and Crump 1994) and *Craugastor escoces* (IUCN, Conservation International, and NatureServe. 2009. Red List of Threatened Species. Version 2011.1. Available from http://www. iucnredlist.org [Accessed 14 Aug 2011]). At intermediate elevations, the stream-dwelling populations seem to be the most affected (Bolaños and Ehmcke 1996) and there are numerous reports of declines in the *Craugastor rugulosus* species group (Campbell 1998; McCranie and Wilson 2002; Lips et al. 2006; Puschendorf et al. 2006b; Bolaños et al.

2008a), the *Craugastor milesi* species group (McCranie and Wilson 2002), and Harlequin Frogs (*Atelopus* spp.; Pounds and Crump 1994; Lips et al. 2003; Puschendorf 2003; La Marca et al. 2005). However, decline and local extinctions of amphibians have occurred also in lowlands in leaf litter species (Whitfield et al. 2007) and stream-breeding species (Puschendorf et al. 2005; IUCN, Conservation International, and NatureServe. 2009. *op. cit.*).

The *Craugastor rugulosus* species group (Savage 1975) consists of 34 stream-associated species with similar ecology (Campbell and Savage 2000; Ryan et al. 2010). Eight species have been described in Costa Rica (Campbell and Savage 2000) but six species have not been observed for the last two decades, including the extinct *Craugastor escoces* (IUCN, Conservation International, and NatureServe. 2009. *op. cit.*). Of these, two species are classified as being Data Deficient, whereas the remaining five are Critically Endangered, including *Craugastor ranoides*, which currently occurs only at the Santa Elena Peninsula (Puschendorf et al. 2005; Zumbado-Ulate et al. 2007).

To develop conservation plans for a species, we first need to characterize its reproductive patterns (e.g., Garton and Brandon 1975; Townsend and Stewart 1994; DiMauro and Hunter 2002) and age-sex population structure (e.g., Hemelaar 1988; Begon et al. 1996; Cogalniceanu and Miaud 2003). There have been few studies on natural history and ecology of species belonging to the *Craugastor rugulosus* group, including work on *Craugastor angelicus* (Hayes 1985) and *Craugastor punctariolus* (Ryan et al. 2008). Such species-specific studies are urgently needed to investigate the effects of emergent diseases and climate change on population structure of endangered species (Donnelly and Crump 1998; Green 2003). Here, we present data on population status and natural history of *Craugastor ranoides* on the Santa Elena Peninsula during a two-year period. These data serve as a comparative framework for establishing long-term monitoring of this species, and also to develop conservation strategies in the near future.

Materials and Methods

Study site.—We conducted this study at Estación Murciélago in the Santa Elena Peninsula, Guanacaste Conservation Area (ACG), Guanacaste, Costa Rica (Fig. 1), which consists mostly of semi-deciduous, tropical dry forest, with a mean annual temperature of 25° C and a mean annual precipitation of 1,500 mm. The climate is seasonal, with a dry period from December to April and a rainy period from May to November. Most small rivers and streams dry up during the dry season, except at springs and deep pools. However, the major rivers flow all-year-round, with their water level increasing significantly during the rainy period.

We located transects for population surveys along three streams: Río Murciélago, Quebrada Pedregal 1, and Quebrada Pedregal 2 (Fig. 1). All three streams were approximately 100 m above sea level, and were similar in that they had a continuous water flow interrupted by small pools. However, Quebrada Pedregal 2 had a larger rocky surface, a greater slope, and more waterfalls. The main substrates available for *C. ranoides* in these three streams were rock-boulders and sediment (i.e., sand, mud, and gravel). An additional substrate was available during the dry season, when leaf litter floated on the water surface. The vegetation was similar along the three transects, with dominant vegetation consisting of Evergreen Tree (*Jacquinia nervosa*, Theophrastaceae), Cabbage Tree (*Andira inermis*, Papilionaceae), Spiny Vine (*Machaerium* sp., Papilionaceae), Panama Tree (*Sterculia apetala*, Sterculiaceae), Licania Tree (*Licanea arborea*, Chrysobalanaceae), Tempisque (*Sideroxylon capiri*, Sapotaceae), and Yellow Plum (*Ximenia americana*, Olacaceae).

Study species.—The riparian frog *C. ranoides* ranges from eastern Nicaragua to western Panama, throughout an altitudinal range of 0–1,300 m. In Costa Rica it has been recorded at lowlands and intermediate altitudes in pre-montane forest, tropical rain forest, and tropical dry forest at the Santa Elena Peninsula, the Caribbean slope, the southern Pacific, and the Central Valley (Savage 2002). However, this species has declined tremendously and remaining populations in Costa Rica are only known from the Santa Elena Peninsula (Sasa and Solorzano 1995; Puschendorf et al. 2005, 2009; Zumbado-Ulate et al. 2007, 2009), where the amphibian pathogen *Batrachochytrium dendrobatidis* has been recently found (Héctor Zumbado-Ulate, unpubl. data). Because of a high risk of extinction, captive breeding has been made a priority for this species (Bolaños et al. 2008b).

Campbell and Savage (2000) reported sexual dimorphism in snout-vent-length (SVL) and tympanum diameter (TD) of adult *C. ranoides*. Males lack nuptial pads, vocal slits, and a vocal sac (Savage 2002). They have been described as mute, but in the course of this study, we heard some males emitting very small and spaced calls. The reproductive ecology of this species and most of the *Craugastor rugulosus* group is unknown, but some reproductive behaviors have been described for *Craugastor angelicus* (Hayes 1985) and *Craugastor punctariolus* (Ryan et al. 2008).

Frog counts.—We conducted field surveys from December 2006 to June 2007 and December 2007 to June 2008. These periods included two dry seasons and the first month of each rainy season. During each dry

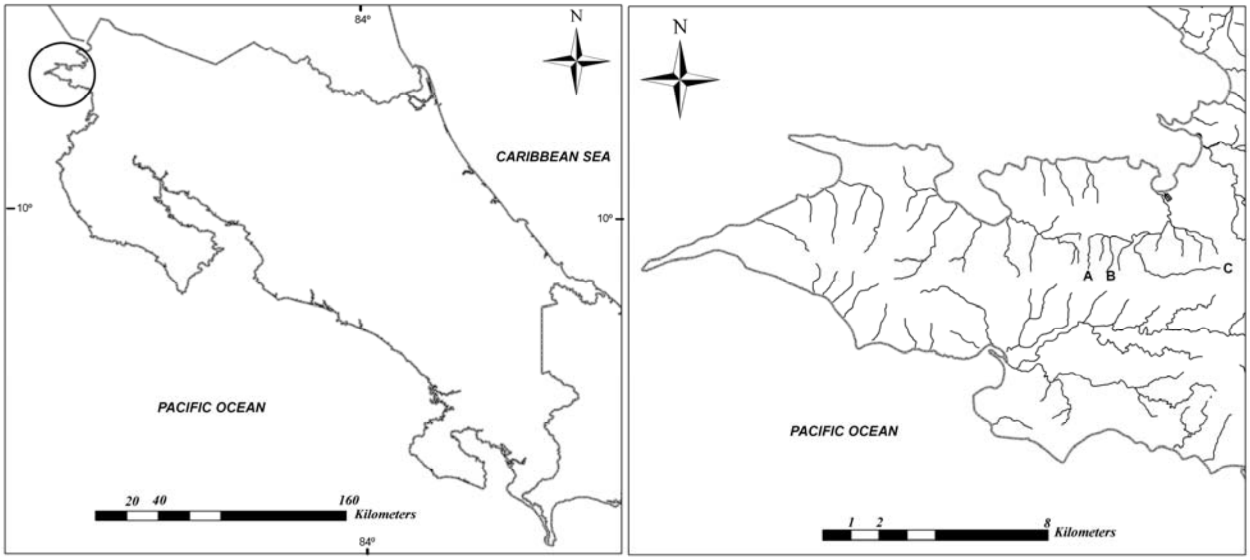

FIGURE 1. Left) Map of Costa Rica showing the Santa Elena Peninsula (circled). Right) Location of the study streams on Santa Elena Peninsula, Costa Rica where populations of *Craugastor ranoides* were monitored 2006–2008:. A) Quebrada Pedregal 1; B) Quebrada Pedregal 2; C) Río Murciélago.

season, we conducted a set of five, three-day surveys in the field and each survey was separated by approximately 45 days. The surveys started at the beginning of the dry season and the last survey coincided with the beginning of the rainy season. We spent one full night on each transect, so we monitored all three streams (total effort: 10 field surveys, 30 samplings, 350 hours). We only surveyed during the period mentioned because the study site becomes inaccessible during most of the rainy season.

We divided each 1,000-m transect into 20 sectors of 50 m. We flagged, numbered, and geographically referenced each section with a global positioning system unit (Garmin® eTrex, Garmin International, Olathe, Kansas, USA). Every survey night, four to six people walked slowly upstream, conducting visual surveys (Lips et al. 2001) from the water's edge to the top of the stream bank. We caught the frogs by hand and put them into clean plastic bags. We measured SVL and TD to the nearest 0.1 mm using a digital caliper (Mitumoyo®), and mass to the nearest 0.1 g using 10- and 50-g scales (Pesola®). We determined sex (male, female, and juvenile) for each individual according Campbell and Savage (2000), who reported sexual dimorphism in TD and SVL, with males having a larger TD relative to SVL than females. Savage and Campbell (2000) considered frogs for which sex could be determined as adults; however, we noticed differences in physical development in these frogs, so we separated them into subadults and adults. We considered male subadults to be males with SVL ranging from 25.0–33.7 mm and mass from 2.0–3.0 g. We classified longer and heavier male frogs as adults. We considered female subadults to be females with SVL ranging from 25.0–39.9 mm and mass from 2.1–5.7 g. We classified longer and heavier females as adults. Frogs with SVL < 25 mm were considered juveniles. We recorded the activity of each frog (motionless, swimming, or jumping), the substrate it was on (rock-boulder, sediment, leaf litter, water or vegetation), and the 50-m sector of transect where it was found.

With data from all sectors, we used Presence 3.1 (Hines, J.E. 2006. Presence 3.1. Software to estimate patch occupancy and related parameters. USGS-PWRC. Available from http://www.mbr-pwrc.usgs.gov/ software/ presence.html [Accessed 11 June 2011]) to calculate the density (abundance along the transect) and the probability of detection of adult frogs between dry seasons and streams using the Royle repeated count model (Royle 2004; Mazerolle et al. 2007), with transects as site covariates. We obtained 95% confidence intervals for both calculations. We did not include juveniles and subadults in the analysis because the model assumes that the system is demographically closed to changes over the course of the surveys (MacKenzie et al. 2006). For these individuals, we designed a multidimensional contingency table, using the season, location, and survey as rows, and the age (juvenile and subadult) as a column. We compared the counts using a log-linear model (model = season + stream + survey + age + season x stream + season x survey + season x age). We summarized the results using a Pearson chi-square test. To compare the adult sex ratio along the five surveys on each dry season, we used a chi-square analysis of contingency tables ($\alpha = 0.05$).

TABLE 1. Counts by age-sex categories of *Craugastor ranoides* in three streams during two consecutive dry seasons (2006–2008) at Santa Elena Peninsula, Guanacaste, Costa Rica.

Dry Season	Stream	Survey	Juv.	Subadult Female	Subadult Male	Adult Female	Adult Male	Total
1	Murcielago	1	5	3	8	4	13	33
		2	4	6	4	2	4	20
		3	3	10	1	2	9	25
		4	7	7	1	4	4	23
		5	0	0	0	0	0	0
	Quebrada Pedregal 1	1	0	1	1	4	0	6
		2	2	2	0	1	1	6
		3	18	1	5	1	3	28
		4	12	1	1	2	1	17
		5	0	0	0	2	2	4
	Quebrada Pedregal 2	1	2	0	0	1	4	7
		2	35	17	8	9	11	80
		3	28	21	4	11	14	78
		4	28	8	10	3	18	67
		5	1	0	0	5	15	21
	Total		145	77	43	51	99	415
2	Murcielago	1	1	16	3	2	6	28
		2	12	40	8	3	9	72
		3	10	29	1	8	2	50
		4	3	12	4	2	5	26
		5	0	0	0	0	0	0
	Quebrada Pedregal 1	1	2	11	3	1	2	19
		2	8	13	5	2	3	31
		3	5	6	0	1	3	15
		4	2	2	1	3	1	9
		5	0	0	0	1	1	2
	Quebrada Pedregal 2	1	4	6	0	8	8	26
		2	17	22	3	20	15	77
		3	9	14	4	11	9	47
		4	3	10	1	12	5	31
		5	0	0	0	7	3	10
	Total		76	181	33	81	72	443

Habitat occupancy and use.—For adult frogs, we designed absence/presence matrices for each dry season and calculated the habitat occupancy and the probability to detect at least one adult individual in every sector on the five different surveys using a single season occupancy model (MacKenzie et al. 2002) performed in Presence 3.1 (Hines, J.E. 2006. *op. cit.*). We excluded juveniles and subadults to fit the model assumption of closed populations (MacKenzie et al. 2002). Additionally, we compared the proportion of substrates used by each age-sex category (juveniles, male, and female) using a likelihood ratio analysis of contingency tables (α = 0.05). For this analysis, we treated the subadults as adults because their sex could be determined.

TABLE 2. Model selection results from repeated count analysis of the frog *Craugastor ranoides* in three streams at Santa Elena Peninsula, Guanacaste, Costa Rica during two consecutive dry seasons. Models used to estimate abundance (λ) and individual detection (p) included the streams as covariates.

Model	AICc	ΔAICc	Number of Parameters (k)	Akaike Weight (w_i)	Dry Season
$\lambda(.)\ p(.)$	604.12	78.34	2	0.10	1
λ (stream) $p(.)$	560.41	6.45	4	0.90	2
$\lambda(.)\ p(.)$	599.45	86.55	2	0.04	2
λ (stream) $p(.)$	551.06	2.56	4	0.96	2

Sexual dimorphism.—We established age-sex categories (adult male, adult female, subadult male, subadult female, juvenile) to compare their mass and size (SVL) using an ANOVA (α= 0.05). For these analyses, we only used data from the second field survey of the second year to avoid recounting individuals, and because we recorded more morphometric data during that survey. However, we considered morphological information from all the surveys when indicating the minimal and maximal values found in the population. To test for sexual dimorphism in TD, we performed an analysis of covariance (ANCOVA; α= 0.05) using the age-sex category (juvenile, male, female) as the dependent variable and SVL as the covariate. The covariance of these two variables was tested with a Tukey test (α= 0.05). We used SYSTAT 11 (SYSTAT Software Inc., Chicago, Illinois, USA) to perform all the statistical tests.

RESULTS

Frog counts.—In total, we caught 858 frogs during the two dry seasons, 417 in the first and 441 in the second (Table 1). Most juvenile and subadult frogs were seen at river edges or near the pools; whereas adults were mainly seen on boulders next to waterfalls. The best model describing the repeated counts in both seasons was the one with streams as covariates (Table 2). Mean density of frogs was 6.36 adults / 50-m sector (SE = 3.07; 95% CI = 0.34–12.38) during the first dry season and 5.87 / 50 m sector (SE = 2.96; 95% CI = 0.07–11.67) during the second dry season (Table 3). In the Quebrada Pedregal 2, mean density of adults per sector and probability of detection were higher than in the other two streams in both dry seasons (Table 3). All the probabilities of detection obtained for every stream were low and ranged between 0.02 and 0.10.

The log-linear model was significant for the proposed model (X^2 = 110.98, df = 44, P < 0.001),

TABLE 3. Estimated density per sector, probability of detection (*p*) and standard error (SE) and 95% confidence intervals (95% CI) for the species *C. ranoides* in three streams (RM = Río Murciélago, QP1 = Quebrada Pedregal 1, QP2 = Quebrada Pedregal 2) during two consecutive dry seasons (2006–2008) at Santa Elena Peninsula, Guanacaste, Costa Rica. The row named as Total, refers to the same parameters but for all the sixty sectors.

Loca-tion	Density (SE)		*p* (SE)	
	Dry Season 1	Dry Season 2	Dry Season 1	Dry Season 2
RM	6.73 (3.52)	5.87 (2.96)	0.07 (0.03)	0.06 (0.03)
95% CI	3.94–30.62	3.56–25.74	0.03–0.16	0.02–0.16
QP1	4.21 (2.28)	4.05 (2.09)	0.04 (0.02)	0.05 (0.02)
95% CI	2.37–19.77	2.40–18.16	0.02–0.11	0.02–0.12
QP2	10.11 (5.17)	9.71 (4.74)	0.10 (0.05)	0.10 (0.05)
95% CI	6.06–44.94	6.08–41.26	0.04–0.23	0.04–0.25
Total	381.77 (184.24)	352.04 (177.54)	0.07 (0.03)	0.06 (0.03)
95% CI	20.66–742.90	4.06–700.03	0.01–0.13	0.01–0.13

indicating the total number of juveniles and subadults varied between the two seasons. We found more juveniles in the first dry season but more subadults in the second dry season (Table 1; $X^2 = 45.02$, df = 1, $P < 0.001$). The counts of juveniles also differed between streams, with more juvenile and subadult frogs counted at Quebrada Pedregal 2 (Table 1; $X^2 = 50.44$, df = 2, $P < 0.001$). Furthermore, counts varied between surveys. There were more juveniles found in the second and third surveys of both dry seasons, and more subadults in the first and second survey of both dry seasons (Table 1; $X^2 = 33.25$, df = 4, $P < 0.001$). We found an adult male-female ratio close to 2:1 throughout the five surveys of the first dry season (Table 1; $X^2 = 1.919$, df = 4, $P = 0.750$); whereas this ratio was closer to 1:1 in the five field surveys of the second dry season (Table 1; $X^2 = 3.97$, df = 4, $P = 0.410$).

Habitat use.—From a total of 60 available sectors, the occupancy was 76% (SE = 0.07) in the first dry season and 84% (SE = 0.07) in the second dry season. The probability to detect at least one individual in every sector during a different survey decreased as the rainy season approached (Table 4). Males, females, and juvenile frogs were most commonly found motionless (Table 5; $G = 2.869$, df = 4, $P = 0.580$) and mainly on boulders (Table 5; $G = 52.36$, df = 8, $P < 0.001$). However, juvenile frogs were more frequently found on leaf litter when compared with males and females (Table 5; $G = 32.68$, df = 8, $P < 0.001$).

Sexual dimorphism.— Adult females were larger ($F_{4,175} = 147.80$, $P < 0.001$) and heavier ($F_{4,175} = 71.95$, $P < 0.001$) than the other age-sex categories (Table 6). The TD increased significantly with SVL (Fig. 2, $F_{1,176} = 112.85$, $P < 0.001$), and this relationship varied between

TABLE 4. Probability of detection (*p*) and standard error (SE) associated with the occupancy of each sector within the transect in different surveys during two consecutive dry seasons for the species *Craugastor ranoides* at Santa Elena Peninsula, Guanacaste, Costa Rica.

Survey	*p* (SE)	
	Dry Season 1	Dry Season 2
1	0.40 (0.08)	0.32 (0.07)
2	0.42 (0.08)	0.56 (0.08)
3	0.46 (0.08)	0.48 (0.07)
4	0.42 (0.08)	0.32 (0.07)
5	0.33 (0.07)	0.24 (0.06)

sexes (Fig. 2; $F_{2,176} = 200.03$, $P < 0.001$). Adult and subadult males had a proportionally larger TD (Fig. 2) when compared with juveniles (*Tukey* = 1.62, $P < 0.001$), and adult and subadult females with the same SVL (*Tukey* = 1.68, $P < 0.001$). The TD of juveniles and females was not significantly different for frogs with a different SVL (*Tukey* = 0.06, $P = 0.860$).

DISCUSSION

The estimated abundance of adults *C. ranoides* showed stable values across two dry seasons in three streams. This apparent stability is consistent with other reports from several streams at the Santa Elena Peninsula (Puschendorf et al. 2005; Zumbado-Ulate et al. 2007). The probability of detection estimated for every dry season and every stream was also stable but low, with a maximum value of $P = 0.100$. This means that individuals that are present within an area will only be observed, on average, once per 10 visits. This result probably reflects the ecology of this species; frogs

TABLE 5. Number of frogs found on each substrate and in each activity class, according to age-sex categories during two dry seasons (2006–2008) at Santa Elena Peninsula, Guanacaste, Costa Rica. Activity categories are Motionless (M), Jumping (J), and Swimming (S).

	Activity			Age-Sex Category		
Category	M	J	S	Juvenile	Female	Male
Substrate						
Rock-boulder	725	34	0	180	344	235
Sediment	6	0	0	2	4	0
Leaf litter	70	12	0	39	36	9
Branches	8	0	0	2	2	2
Water	0	0	3	0	2	1
Age-Sex						
Juvenile	212	11	0			
Female	362	24	2			
Male	235	11	1			

TABLE 6. Mean (standard error) of snout-vent length (SVL) and mass of different age-sex categories of *Craugastor ranoides* at Santa Elena Peninsula, Guanacaste, Costa Rica.

		SVL (mm)			Mass (g)		
Age-Sex	N	Mean	Min.	Max.	Mean	Min.	Max.
Juvenile	37	20.86 (0.77)	8.3	24.0	1.07 (0.54)	0.5	2.5
Subadult-female	75	31.65 (0.54)	25.4	39.9	3.52 (0.38)	2.1	5.7
Subadult-male	16	28.96 (1.17)	25.0	33.7	2.49 (0.82)	2.0	3.0
Adult-female	25	49.16 (0.94)	40.0	70.3	14.49 (0.66)	6.2	34.0
Adult-male	27	37.60 (0.90)	33.9	45.4	6.16 (0.63)	5.5	10.0

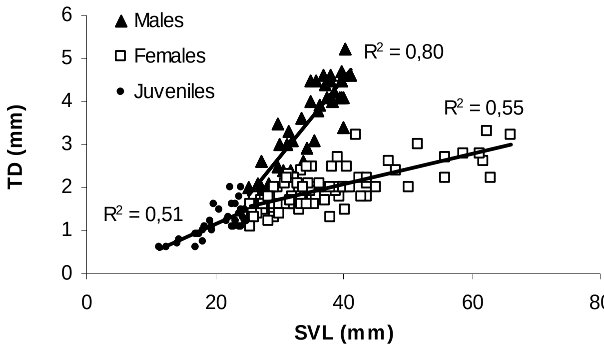

FIGURE 2. Sexual dimorphism in tympanum diameter (TD) and snout-vent length (SVL) in *Craugastor ranoides* at Santa Elena Peninsula, Guanacaste, Costa Rica.

usually clump near pools and waterfalls. In such places, individuals hide under rocks or remain motionless, rendering themselves well camouflaged against leaf litter or boulders, which makes them difficult to find and, therefore, count. Moreover, because calls are almost imperceptible, acoustic surveys for this species are useless. We suggest that low detectability is a pattern shared by most species of this clade and is one of the main reasons why amplectant pairs or egg clutches have rarely been observed.

The abundance of *C. ranoides* differed between neighboring streams in the same region. These results are similar to those of Ryan et al. (2008), who reported a significant difference in the abundance of frogs of *Craugastor punctariolus* in neighboring streams that were similar in habitat characteristics. Perhaps we counted more frogs in Quebrada Pedregal 2 because it has a greater slope, which produces more waterfalls and pools where adult frogs might clump. However, slope was not measured along the surveys, so it was not included as a covariant in the statistical analysis. Clumping in such microhabitats is very common for stream breeding species (Wilson and McCranie1985, Pounds and Crump 1987; Tsuji and Kawamichi 1996) and these aggregations might have been even stronger because waterfalls and adjacent pools acted as water reservoirs that provide suitable habitat during the entire dry season, when most of the river is dry. We also found forest-dwelling (*Craugastor fitzingeri*) and pond-dwelling (*Leptodactylus melanonotus* and *L. poecilochilus*) frogs clumped in these same sites during the dry season.

The counts of juveniles and subadults showed similar patterns, with more frogs found at Quebrada Pedregal 2, where a higher density of adults was also estimated. We cannot explain why there was a difference in the number of juveniles and subadults between successive surveys, or why this pattern was reversed for juveniles and subadults. It would be necessary to monitor the population through several more seasons to determine if these trends were random or if they truly represent demographic and reproductive patterns. We recommend that future studies increase the number of surveys at each site during each monitoring period so that a multiple-season occupancy model can be applied (MacKenzie et al. 2006).

Within the *Craugastor rugulosus* group, only the study by Ryan et al. (2008) has looked at sex ratios, and they reported a 1:1 male-female ratio for *Craugastor punctariolus* across two consecutive years. In the present study, a male-female ratio of approximately 2:1 was observed during the first dry season and a ratio closer to 1:1 was observed during the second dry season. We suggest two possible explanations for this change. During the study we noticed that females were more difficult to catch than males, and that they moved faster across the streams when escaping. Possibly, several females escaped in the first season, when we were learning sampling techniques. Alternatively, our data could indicate a reproductive peak during the first dry season, with males displaying in a clumped manner. During all 10 surveys, we found more adults near waterfalls, so we suggest that adult males probably display and mate in these habitats, which is common for other stream-breeding frogs (e.g., Pounds and Crump 1987; Tsuji and Kawamichi 1996). Unfortunately, the reproductive behavior of this species is completely unknown and more research is needed to test this idea.

Habitat occupancy was high in both seasons and ranged between 76% and 84%. Also, in most surveys we obtained a high probability of detecting at least one individual at each site during the same season. This pattern shows that frogs are spaced along the entire transect, but that the occupancy did not reach 100% because several sites were dry during most of the dry season. The probabilities of detection decreased noticeably at the end of the dry season. During the rainy season, stream-breeding frogs move away from the streams and into the forest to get protection from sudden increases in the water flow, and this can directly influence our ability to detect frogs. On numerous occasions on rainy nights in June 2007 and 2008, we observed adult frogs moving several meters away from the river, and even along the road that runs perpendicular to the streams. Possibly, strong water flow drags frogs downstream, causing injury or death. During a night of heavy rain in January 2007, two juveniles were observed on branches 2 m above the stream. This is particularly interesting because behavioral adaptations to avoid getting dragged by rapid water flow have not been reported for this species. Equally possible, the high levels of water decreased our ability of finding and catching the frogs. As an apparent ecological feature of the *Craugastor rugulosus* species group, Savage (2002) states that a decrease in detection of these species during the rainy season is common.

We found that juvenile *C. ranoides* use different substrates than males and females, similar to that reported for *Craugastor punctariolus* (Ryan et al. 2008). Most frogs were observed motionless on boulders, a behavior apparently common for species within the *Craugastor rugulosus* group (Savage 1975, 2002, Campbell 1998, Campbell and Savage 2000, McCranie and Wilson 2002).

The morphometric results for juveniles and adults were consistent with those reported by Campbell and Savage (2000). However, we included the mass as another variable to distinguish between age-sex categories. We also established another age-sex category (subadult) based on morphological measurements. This information should help distinguish between age-sex categories with more precision in future ecological studies. As in most anurans and in all species of the *Craugastor rugulosus* group, females were generally larger and heavier than males (Campbell and Savage 2000; Savage 2002). Sexual dimorphism in TD in frogs is generally associated with the existence of advertisement call in males (Brenowitz et al. 2001, Kelley et al. 2001). Even though males of *C. ranoides* are assumed to be mute (Savage 2002), the remarkable sexual dimorphism observed in tympanum size suggests males might produce vocal sounds, and during this study, we heard males calling during at least five occasions. When a call occurred, the male emitted only a single note.

The number of *C. ranoides* found during field surveys in the Santa Elena Peninsula remained stable across two consecutive years. However, because of their Critically Endangered status, we recommend continued monitoring and an increase in the number of surveys at each site. Increased monitoring would also help elucidate the reproductive ecology of this species and the detection of possible fluctuations in the abundance of age-sex categories. Here, we provide as a first step information on natural history, density, detection estimations, and morphometric data that could be used by zookeepers when implementing *ex situ* conservation strategies for this species. Additionally, this study illustrates the urgent need for conserving the tropical dry forest at the Santa Elena Peninsula where the only remaining populations of *C. ranoides* survive. The disappearance of this ecosystem would likely lead to the extinction of *C. ranoides*.

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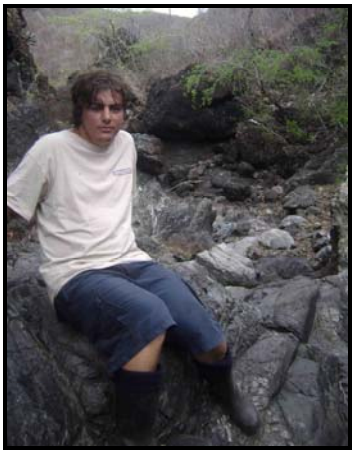
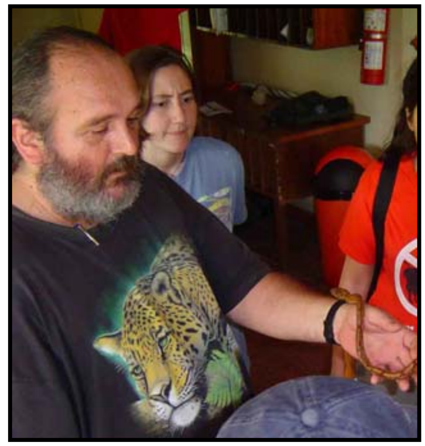


HECTOR ZUMBADO-ULATE recently completed his M.S. degree in the School of Biology at the Universidad de Costa Rica, where he studied the distribution and population ecology of the frog *Craugastor ranoides*. He also worked on detecting the chytrid fungus *Batrachochytrium dendrobatidis* in the tropical dry forest of Costa Rica. Both studies formed part of his thesis. He is most interested in monitoring amphibian populations in decline, but he conducts research on other herpetological topics. Currently, he is a full time Professor in the School of Biology at Universidad de Costa Rica, where he teaches courses related to amphibian ecology and conservation biology. In the near future, he plans to pursue a Ph.D. in zoology or conservation biology. (Photographed by Daniela Corrales)



FEDERICO BOLANOS received his M.S. degree in Biology at the Universidad de Costa Rica (UCR). Most of his research projects have been conducted on the biology, systematic, and conservation of amphibians, but he has also worked on reptile ecology and conservation. He has been the mentor of more than 23 Master's degree students. Currently, he is a Professor in the School of Biology at UCR and Curator of the herpetological collection in the Zoology Museum at UCR. In the last decade, he has actively participated in the Research and Analysis Network for Neotropical Amphibians (RANA). Moreover, he is a member of the Amphibian Specialist Group (ASG) and the Conserving Breeding Specialist Group (CBSG) of IUCN. He has written more than 40 publications including book chapters and peer-reviewed papers in scientific journals. (Photographed by Bruce E. Young)

BEATRIZ WILLINK is a Master's student at University of Costa Rica where she received her B.S. in Biology. Her undergraduate work focused on seasonal fluctuations and long-term changes in tropical leaf-litter herpetofauna. She is currently on an internship at the Smithsonian Tropical Research Institute, studying the trade-offs associated with hatching plasticity in the Red-Eyed Tree Frog (*Agalychnis callidryas*). She is interested in tropical herpetology, specifically lethal and non-lethal interactions with predators, dispersal, demographic fluctuations, and how these processes are influenced by the environment and by the transitions across complex life cycles. Her goal is to continue her graduate studies and pursue a Ph.D. (Photographed by Julie Charbonnier)

FERNANDO SOLEY-GUARDIA finished his B.S in biology in 2003 at the Universidad de Costa Rica (UCR). Currently, he is pursuing a Ph.D. at Macquarie University in Sydney, Australia. He is most interested in animal behavior. His thesis project deals with the life history, behavior, and ecology of assassin bugs in Australia. His project has combined expansive field studies at numerous sites in the Northern Territory and Western Australia, as well as detailed laboratory studies. (Photographed by Fernando Soley-Guardia)