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Sexual Dimorphism in *Osornophryne guacamayo* with Notes on Natural History and Reproduction in the Species

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Osornophryne guacamayo is distributed between 1800 and 2200 m on the eastern slopes of the Andes and adjacent foothills in central Ecuador. Few specimens have been discovered since the species was described (Hoogmoed, 1987), and information regarding variation within the species and among sexes, habitat preference, reproduction, and diet are limited. Ruíz-Carranza and Hernández-Camacho (1976) included some aspects of the natural history and reproductive biology of *Osornophryne* in their description of the genus. Cannatella (1986), Hoogmoed (1987), and Gluesenkamp (1995) also reported briefly on general habitat attributes and microhabitats in which other species were encountered. Stomach contents were reported for some species by Ruíz-Carranza and Hernández-Camacho (1976) and by Gluesenkamp (1995).

Many species of the genus *Atelopus*, hypothesized to be most closely related to *Osornophryne* (Cannatella, 1986; Graybeal, 1995; Coloma, 1997), have recently undergone drastic population declines the causes of which are still unknown. Understanding the natural histories of these taxa may provide information leading to a better understanding of the causes of these declines. We present for the first time data on male morphology, season of reproduction, vocalization, and reproductive behavior in *Osornophryne guacamayo*. Further data are presented regarding ontogenetic color variation in females, microhabitat preference, sexual dimorphism, and diet of this species.

Individuals were collected primarily on Volcán Sumaco and Volcán Reventador and in the Cordillera de los Guacamayos. A few specimens collected at other localities have been included in this analysis.

Microhabitat data for populations from Volcán Sumaco, Cordillera de los Guacamayos, and Volcán Reventador were recorded in July and August 1992 and March and April 1996. Microhabitat descriptors scored included substrate (leaf, branch, trunk of tree, ground), and perch size. Perch classes were defined as Short = leaf < 15 cm in length; Medium = leaf 15–30 cm; Long = leaf > 30 cm; Bromeliad = arboreal bromeliad of any size. Color pattern and morphometric data were recorded for all available specimens. Some microhabitat descriptors were recorded for individuals that were not collected. These individuals are included as “unknown” in all analyses with the exception of 15 large (> 30 mm SVL) individuals with yellow venters which were assumed to be adult females based on the distribution of these traits among specimens of known sex. Color pattern and size was not recorded for all individuals encountered. Therefore, the unknown class likely contains some adult females. Overall, the observed sex ratio was skewed toward adult females which accounted for 35 of 106 individuals observed (including 17 juvenile females, 20 males, and 34 individuals of unknown gender).

Nearly all specimens were collected on vegetation at night (Fig. 1). Five specimens (four adult females and one male) were encountered walking on the ground during the day. Individuals of both sexes perched at various perch heights with no differences apparent among sex or age classes with the exception that only adults were found on the ground (Fig. 1). A single adult female was collected in an epiphyte 20 m above the ground and two others on the ground under

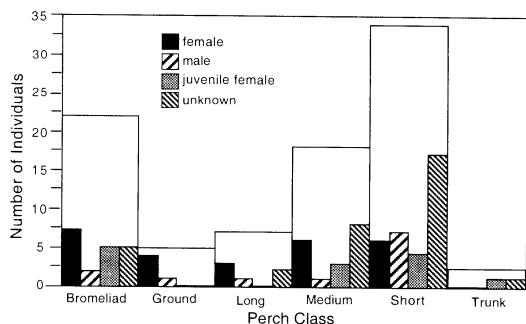


FIG. 1. Distribution of age/sex classes among perch classes.

roadside rocks, indicating that this species occupies microhabitats outside of those most heavily sampled.

Osornophryne guacamayo appears to be a generalist predator of a wide variety of invertebrates (Table 1). Stomachs from 20 individuals were examined and 12 (one juvenile female, seven adult females, and four adult males) were found to contain prey items. The presence of mineral sand and soil in the stomachs of three adult females suggests that they occasionally forage on the ground.

Sex was determined by examination of the gonads as well as presence or absence of a nuptial excrescence. Females, as well as males, possessed ventrally directed cloacal tubes. These tubes appeared to be highly flexible and were sometimes difficult to observe, depending on the position of the individual, especially after preservation.

Adult females had a bright yellow, tuberculate venter, frequently patterned with black spots or marbling. Some individuals had broken or nearly complete yellow dorsolateral lines and a single, black midventral line. A few adult females collected at each locality had a greenish dorsum with black tubercles and large yellow patches with irregular borders scattered about the dorsum. Adult females usually had a dark dorsum sometimes with small, irregular yellow patches. Three individuals from Sierra Azul differed in having a yellowish brown dorsum with a creamy yellow venter. Healed bite marks were visible on the dorsum of a single adult female from Volcán Reventador. All females had red palmar and plantar surfaces that were displayed during unken reflex. Dorsal skin texture was slightly to highly tuberculate. Extremely small juvenile females (SVL < 10 mm) were likely recent hatchlings and had black venters spotted with cream-colored flecks. In larger, subadult females, the venter was dark brown or black with scattered, low, yellow tubercles, especially in the ventrolateral region and on the flanks. There appeared to be a drastic change in ventral coloration with the onset of sexual maturity in females. Large yellow blotches with irregular borders replaced dark areas among ventral tubercles and frequently fused to completely cover the venter. A single adult female from Volcán Sumaco had a black venter.

Males were identical to subadult females in skin coloration and body size. Males had a dark brown or black dorsum, occasionally with tan or yellow dorsolateral lines. Dorsal skin texture was weakly to highly

TABLE 1. Stomach contents of *Osornophryne guacamayo* (N = 12 individuals; one juvenile female, seven adult females, and four males).

Prey category	Number of prey items	Number of frogs with prey
Isopoda	3	2
Diplura	1	1
Annelida	1	1
Coleoptera	30	10
Larva	2	2
Curculionidae	4	4
Diptera	13	2
Hymenoptera	1	1
Formicidae	33	3
Diplopoda	2	1
Orthoptera	14	5
Blattaria	1	1
Homoptera	5	4
Heteroptera	1	1
Insect egg	2	2
Pseudoscorpiones	1	1
Aranea	6	4
Acari	7	4
Leaf matter	3	3
Mineral sand/soil	2	2

tuberculate. Palmar and plantar surfaces were red. Males had obvious nuptial excrescences on the skin overlying the outer margin of the first metacarpal. Both sexes had numerous low warts on the palmar surfaces, including paired, subdigital, articular warts. However, the palmar surface in males was covered by larger, and fewer, warts and did not have the finely rugose texture seen in adult females.

Morphological measurements were made using digital calipers. Abbreviations are as follow: SVL = snout-vent length; TIB = tibia length; FOOT = length of foot from base of inner metatarsal tubercule to tip of fourth toe; HWID = greatest width of head; HLEN = length of head from posterior margin of jaw to tip of rostrum; IOD = interorbital distance; IND = inter-narial distance; EN = distance from anterior margin of orbit to posterior margin of nostril; ED = diameter of eye; NR = distance from anterior margin of nostril to tip of rostrum; EW = widest width of upper eyelid measured perpendicular to medial axis of skull; LAC = Luis A. Coloma field series; AGG = Andrew G. Gluesenkamp field series; QCAZ = Museo de Zoología, Departamento de Ciencias Biológicas, Pontificia Universidad la Católica del Ecuador.

Sexual size dimorphism is extreme in this species with females nearly always larger than males (pooled variances $t = 2.91$, $df = 33$, $P = 0.010$, $N = 35$, Fig. 2). Statistical analysis of 11 morphometric variables was conducted to determine whether observed differences between the sexes are the result of differentiation by both sexes or whether they can be accounted for by a shift in ontogenetic trajectory by one sex. A MANCOVA using SVL as the covariate detected no significant differences between the sexes in the regression slopes of any variables for 27 females and eight males. However, all analyses suffered from low power (0.050–0.242), indicating that the probability of

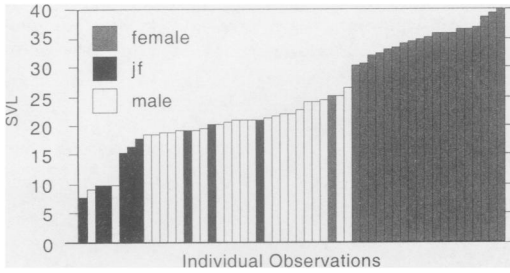


FIG. 2. Distribution of SVL among age/sex classes.

a type I error is high in this dataset. A simple bivariate plot of morphometric variables regressed over SVL (Fig. 3) illustrates the linear relationship between size and shape among individuals. These results suggest that sexual dimorphism in this species is a result of the extended growth trajectory of females and that males are not significantly different in size or shape from juvenile females.

An amplexant pair as well as a single clutch of eggs were encountered in the field at the beginning of the rainy season (March to April). Several very small juveniles (SVL < 10mm) were encountered during mid-June and early August, although none was observed during earlier months. Inguinal amplexus, previously described in *O. percassa* and *O. bufoniformis* (Ruiz-Caranza and Hernández-Camacho, 1976) was observed among *O. guacamayo* in the field and in the laboratory. Pairs collected in March and August readily entered amplexus in the lab; however, it is unclear what influence captivity had on reproductive behavior.

A single clutch of eggs (LAC 2199, deposited in QCAZ) was collected from under a roadside rock in March 1990 by L. Coloma and J. Wiens. The clutch contained approximately 50 eggs with thick, yellowish brown capsules ranging from approximately 4.0–6.0 mm in capsule diameter. Mating between two captive individuals in August 1992 produced a clutch of 35 large eggs (4.06–5.50 mm capsule diameter, 2.61–3.30 mm egg diameter, QCAZ 1270) deposited in moss in a laboratory terrarium. All eggs had thick, yellowish brown capsules, and yellowish yolks. The eggs were preserved in 10% formalin after apparent fungal infection (L. Coloma, pers. comm.). Four eggs (two of the largest and two of the smallest in the clutch) were dissected, and all appeared to be at blastula or gastrula stage with some cleavage/blastomere visible.

Call recordings were obtained in the Cordillera de los Guacamayos, Provincia del Napo, approximately 8 km east of Cosanga on the Quito–Tena road, at an altitude of 2200 m. Recording equipment included a Marantz CP 430 stereo cassette recorder, a Sennheiser ME 66 directional microphone and a Sony SR metal tape. An audiospectrogram and oscillogram were analyzed using Canary[™] and Soundedit[™] to generate audiospectrograms and oscillograms and to obtain mensural information on the spectral and temporal characteristics of the calls from two recordings from a single male (AGG 346, deposited in QCAZ). Digitization and editing of vocalizations were completed with a Macintosh Power PC 7100/80AV at a sampling frequency of 44.1 KHz and 8 bit resolution with Sound

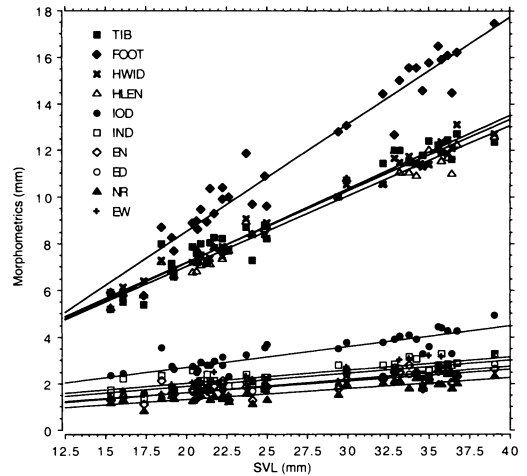


FIG. 3. Bivariate plot of morphometrics showing linear relationships between size (SVL) and shape.

Edit Pro[™] and Sound Effects[™] programs. The terminology follows that of Croft and Ryan (1995).

The call presented here (Fig. 4) represents the first record of vocalization in genus. An adult male specimen began to vocalize after being placed in a plastic container with an adult female. Both specimens were immediately placed on the ground near the point of capture and vocalization proceeded. The male called only when in very close proximity or direct contact with the female. Call parameters were recorded from two bouts of calling and include call length (\bar{x} = 289.567 ms, SD = 16.169), number of pulses (\bar{x} = 16.83, SD = 1.179), pulse rate (\bar{x} = 0.057/ms, SD = 0.002), pulse length (\bar{x} = 1.595 ms, SD = 0.441), and dominant frequency (\bar{x} = 3.185 KHz, SD = 0.040). Temporal and spectral characteristics of the call indicate that it was produced primarily by passive amplitude modulation (Martin, 1972).

It is possible that, given the absence of internal or external hearing structures in this species and the low intensity of the call, that individuals may communicate via direct contact, that is, vibrational rather than acoustic signaling. We assume that the low amplitude croaks emitted by the male form a part of courtship in this species.

Developmental mode in *Osornophryne* is unknown. However, several factors suggest that the eggs of *O.*

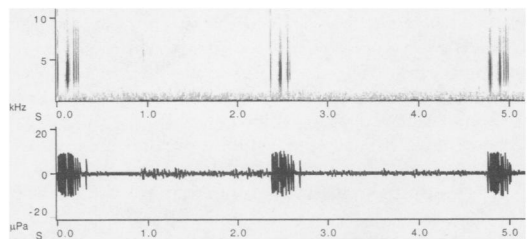


FIG. 4. Sonogram and oscillogram of call of male *Osornophryne guacamayo* (AGG 346, deposited in QCAZ).

guacamayo undergo direct development. Terrestrial deposition of large, unpigmented eggs in sites without available aquatic nesting sites has also been reported for *Oreophrynella quelchii*, a direct developing species from the tepuis of the Guayanan Highlands (McDermid and Gorzula, 1989). Apparent hatchling individuals have been encountered in the field, but larvae or aquatic eggs have never been found. *Osornophryne* typically occur in places where aquatic breeding sites are uncommon or absent, and adults are unable to swim according to Ruiz-Carranza and Hernández-Camaacho (1976) and laboratory observation with *O. guacamayo*. Therefore, we suggest that *O. guacamayo* is a direct developer.

Adult female *O. guacamayo* are more likely to be encountered in exposed areas (on larger leaves or on the ground) than other sex or age classes. In addition to hatchlings encountered during summer months, two size classes of females were typically present in populations sampled: large, colorful adults and smaller, drab subadults, which are indistinguishable from adult males. Lindquist and Hetherington (1998) described an ontogenetic shift in color pattern in the toad *Atelopus zeteki*. Recent metamorphs and subadults are cryptically patterned with dorsal coloration matching background color and occupy less exposed microhabitats than adults. Adults are brightly colored with immaculate yellow or patterned dorsums. We hypothesize that juvenile coloration and behavior may be correlated with a lack of skin toxicity sufficient for deterring predators.

Although *O. guacamayo* appears to be a generalist predator throughout its ontogeny, it is possible that skin toxins accumulate with age (Lindquist and Hetherington, 1998) because likely sources of precursor alkaloids (formicids, and coleoptera) are consumed by all age classes (Table 1). Color dimorphism associated with size in this species may indicate a trade-off between predator-avoidance and antipredator mechanisms (Brodie et al., 1991; Hileman and Brodie, 1994). Aposematic coloration in adult females may serve as an antipredator mechanism whereby they are able to advertise increased skin toxicity associated with age or size to deter predators rather than rely on predator avoidance alone.

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Reproductive Ecology of the Ploughshare Tortoise (*Geochelone yniphora*)

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