Desmognathus brimleyorum, and a comparison with other desmognathine salamanders. J. Zool. 243:21–27.

APPENDIX 1. Collection data for specimens examined.

Species	Museum No. (ASUMZ)	Date of collection (mm/dd/yy)	SVL (mm)	County
P. albagula	22419	4/17/98	70	Crawford
P. albagula	15887	4/14/90	72	Crawford
P. albagula	15464	3/13/90	71	Newton
P. albagula	22756	5/27/98	72	Polk
P. albagula	19201*	9/22/93	62	Pike
P. ouachitae	22762	5/27/98	56	Polk
P. ouachitae	24016	4/15/00	60	Polk
D. brimleyorum	22397	3/27/98	68	Montgomery
D. brimleyorum	21840	5/11/97	76	Polk
D. brimleyorum	22523	4/18/98	84	Polk
D. brimleyorum	21749	4/19/97	85	Polk
D. brimleyorum	23156	4/16/99	79	Logan
D. brimleyorum	3561**	8/15/80	89	Polk

*Animal collected during non-reproductive season.
**Animal collected during non-reproductive season; skin only excised from dorsal trunk region.

Reproductive Ecology of *Atelopus zeteki* and Comparisons to Other Members of the Genus

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The Panamanian Golden Frog, *Atelopus zeteki* Dunn (Anura: Bufonidae), is a taxon of concern endemic to the Coclé and Panamá Provinces of Panama (Dunn 1933; Savage 1972), principally inhabiting lowland rainforest (Savage 1972) on the Pacific cordilleran slope. Bufonidae are among four families of amphibians containing more "rapidly declining" species than the average (Stuart et al. 2004), and of 34 species of amphibians which have gone extinct since 1500 (Stuart et al. 2004), three were in the genus *Atelopus* (IUCN et al. 2004). In addition, of 77 described species of *Atelopus* (Frost 2004), 61 (82%) are listed as Critically Endangered (IUCN et al. 2004), and it has been suggested that this is the first example of a species-rich lineage being so uniformly imper-

iled (Lötters et al. 2004). In particular, *Atelopus zeteki* is listed as Critically Endangered (IUCN et al. 2004) and given the highest level of protection by the Convention on International Trade in Endangered Species (CITES I). Development of conservation strategies and long-term monitoring programs for threatened species is contingent upon understanding species' life histories. As basic biological and ecological information is lacking for many *Atelopus* species, collection of such data may be crucial for conservation efforts.

Relatively little is known about the reproductive ecology of *Atelopus* frogs (Lötters 1996). While breeding phenology usually varies somewhat among species and populations depending upon local climatic conditions, limited data suggest that *Atelopus* breeding generally occurs at the beginning of the dry season (Lötters 1996, Savage 2002). *Atelopus* oviposit in cryptic locations, attaching their eggs to the undersides of rocks in swiftly flowing streams generally during periods of low water flow (Savage 1972, Lötters 1996). Previous descriptions of egg-laying and clutch characteristics come principally from captive or dissected animals. The few reported field observations of egg masses or oviposition sites provide limited data on clutch sizes, ovum diameter, and/or oviposition site characteristics in *A. flavescens* (Lescure 1981) and *A. franciscus* (Boistel et al. 2005) from French Guyana, and *A. muisca* (Rueda-Almonacid and Hoyos 1991) from Colombia. To our knowledge, no published information from the field or laboratory exists on the reproductive ecology of *A. zeteki*. Our objectives were to describe the clutches and oviposition sites of *A. zeteki* and compare their reproductive ecology with that of other *Atelopus* species.

Materials and Methods.—In 10–16 December 2004 and 8–15 December 2005, we conducted surveys for *Atelopus zeteki* in Panamá Province, Panama, in a small stream ca. 5–15 m in width with steep rocky slopes. We searched for *A. zeteki* egg masses by overturning rocky substrates and submerged woody debris and examining accumulations of leaf litter within the stream channel along a 200 m reach. These searches were conducted in conjunction with surveys for adult *A. zeteki* along the stream margins and on exposed rocks and small islands within the stream. All frogs were marked by toe-clipping. When clutches were found, we counted the number of eggs per clutch and measured the diameters of at least 20 eggs, randomly chosen, from each of three clutches. Embryo developmental stages were estimated (Gosner 1960). To characterize the microhabitat at oviposition sites, we measured overstory canopy closure using a concave spherical densiometer (only in 2005), size of substrate (Platts et al. 1983) to which an egg mass was attached, predominant size of surrounding substrate (visually estimated within a 1 m² area centered on the oviposition substrate), water depth at the location of the clutch (only in 2004), distance of oviposition substrate to wetted edge, wetted width of stream at each oviposition site, stream velocity (m/s) near each egg mass, and instream habitat type (e.g., pool or riffle, Platts et al. 1983). Stream velocity at oviposition sites was estimated by determining the time it took for a floating object to travel a 1 m stream segment centered on the location of an egg mass. Velocity was calculated as the distance traveled divided by the time elapsed. In addition, we measured the distance between clutches within each year. In 2004, we measured general habitat conditions for five of the variables along the stream reach and

compared these with microhabitat characteristics at oviposition sites using Student's t-tests. Canopy closure was measured at the beginning and every 10 m along the reach within one m of the stream margin and averaged. We visually estimated the proportion of the surface of the streambed made up of cobble, gravel, pebble, sand, and silt (after Platts et al. 1983) within 20 randomly located 1-m wide bands that bisected the reach. Water depth was measured at three equidistant points across the width of the stream at 20 randomly selected locations along the 200 m reach. Depth measurements were averaged. We determined mean wetted width from measurements at 20 randomly selected locations along the reach. Stream velocity was measured within one meter of the margin at 20 randomly selected locations along the reach and averaged.

Results.—Over two breeding seasons, we found 17 clutches of eggs of *A. zeteki* within the 200 m-long reach and one clutch upstream of the reach. In 2004, we found 41 amplectant pairs, 208 single frogs, and seven clutches of eggs of *A. zeteki* during five surveys over a seven-day period. In 2005, we found four pairs, 166 individuals, and 11 clutches in five surveys over eight days. Each intact clutch appeared to contain a single strand of small, cream-colored eggs attached to a rocky substrate in the stream (Table 1). Strands were attached to the substrate and then wrapped back up on themselves creating two or more layers of eggs in a loose, elongated mass (Fig. 1). In 2004, most of the clutches found

Fig. 1. Clutch of *Atelopus zeteki* attached to boulder in Panamá Province, Panama. Photo by N. Karraker.

appeared to have been recently oviposited, but in 2005 many of the clutches had begun hatching or had already hatched. Accurate counts of clutch size were made for five clutches in 2004 and four in 2005. Mean clutch size was 370 ± 137 (SD) (N = 9; Table 1). Eggs ranged in developmental stage from cleavage to hatching. We were unable to determine the duration of embryonic development in the field. But in captivity, the embryonic period of *A. zeteki* ranged 7–11 days at 22.0°C and averaged 8.9 ± 1.3 days (N = 9) (Detroit Zoo, unpubl. data).

Embryos averaged 1.8 ± 0.2 mm in diameter (range 1.4–2.5 mm, N = 60). Mean water temperature at oviposition sites was 23.4 ± 0.8°C (N = 15). On 11 December 2004, pH of the stream was 7.8. Six clutches were attached on the top, one on the side, and 11 on the undersides of substrates. All but one clutch were attached to cobble- or boulder-sized substrates (Table 1). All clutches but one were found within 2 m of the stream margin and were evenly distributed between riffle and run habitats. Percent canopy closure was lower (t = 2.04, P = 0.050) above oviposition sites at 93.1 ± 5.8 (range 85–100; N = 9), while the average for the reach was 96.9 ± 1.9 (range 91–99; N = 21). Sand was the predominant substrate type around oviposition sites for 15 of 18 (83%) clutches, while the proportions of surface substrates overall within the reach were 36% cobble, 31% sand, 20% pebble, 6% gravel, and 7% silt (N = 20). Water depth at oviposition sites averaged 16.5 ± 15.7 cm (range 1–44; N = 6), and was lower (t = 2.44, P = 0.022) than the average depth for the reach of 30.8 ± 11.0 cm (range 17–63; N = 20). Mean wetted width of the stream at oviposition sites was 9.9 ± 3.7 m (range 6.1–18.7; N = 15), and was higher (t = 2.94, P = 0.006) than the reach average of 7.7 ± 2.1 m (range 4.2–11.8; N = 20). Mean stream velocity at oviposition sites was 0.34 ± 0.15 m/s (range 0.10–0.50; N =15), and comparable (t = 0.74, P = 0.463) to the average for the reach of 0.37 ± 0.10 m/s (range 0.23–0.50; N = 20). Two clutches were separated from others by 22 m each, but the mean nearest neighbor distance between all other clutches within the reach was 1.1 ± 1.3 m (N = 15). Two clutches were found attached to the underside of the same boulder, 11 and 12 cm apart, in 2004 and 2005, respectively. In 2005, we found two clutches attached 12 cm apart on the underside of another boulder. Aside from the single clutch found upstream of the reach, all clutches in both years were located within a 25-m reach of stream.

Seven clutches were no longer submerged under water when found and one appeared to be covered by a white fungus. It had rained heavily in the area just prior to surveys each year, so presumably these exposed clutches were oviposited when the water level was higher in the stream.

Discussion.—We observed eggs of *Atelopus zeteki* in December 2004 and 2005, which marks the transition between rainy and dry seasons in most years. We observed amplectant pairs as early as 8 December in 2005 and as late as 25 January in 2004. Surveys of this site, associated with a separate study on population dynamics, in February, March, July, and August yielded no amplectant pairs. Small, but well-developed, larvae were observed in the stream in mid-December 2005, but no metamorphs or subadults were found, indicating that the breeding season probably begins in late November or early December and continues into January. Further evidence comes from observations made on 4 December 2003, in which no adults were observed along the stream, but males
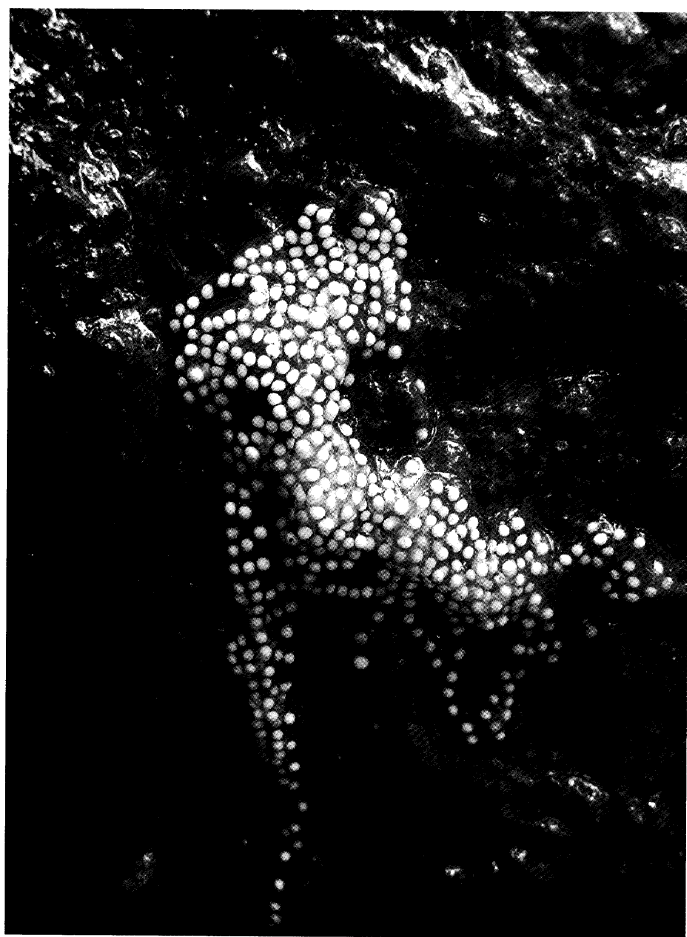
TABLE 1. Clutch sizes, developmental stages (after Gosner 1960), and characteristics of oviposition sites of *Atelopus zeteki* observed in Panamá Province, Panama. Substrate size categories: silt (<0.06 mm), sand (0.06 to 2 mm), gravel (2 to 64 mm), cobble (64 to 256 mm), boulder (256 to 4096 mm), and bedrock (>4096 mm), as measured across the longest diameter (Platts et al. 1983). Habitat types follow Platts et al. (1983). — Indicates data were not collected. [1]Indicates clutches for which accurate counts could not be made. [2]Indicates clutches in which all other eggs appeared to have hatched.

Clutch size	Stage of development	Canopy closure	Water temp. (°C)	Substrate type	Surrounding substrate type	Distance from stream margin (cm)	Water depth (cm)	Habitat type	Stream flow (m/s)	Wetted width (m)
327	cleavage	—	24.2	cobble, boulder	sand	0	10	riffle	0.20	6.9
256	cleavage	—	22.5	bedrock	sand	0	44	run	0.10	10.4
243	cleavage	—	22.5	cobble	sand	0	1	run	0.10	10.6
no count[1]	hatching	—	22.5	boulder	gravel, cobble	77	10	run	0.33	8.8
202	cleavage	—	22.5	cobble	cobble, boulder	0	8	run	0.33	8.9
72[1]	hatching	—	22.5	boulder	sand	76	26	run	0.33	15.7
481	neurulation	—	22.5	boulder	sand	76	26	run	0.25	18.7
48[1]	none evident	99	23.2	boulder	sand	92	—	run	0.50	14.8
465	hatching	100	23.6	boulder	sand	55	—	run	0.50	14.8
623	organogenesis	100	23.6	boulder	sand	67	—	run	0.50	8.9
416	hatching	96	23.6	boulder	sand	54	—	riffle	0.50	6.1
318	none evident	97	23.1	boulder	sand	35	—	riffle	0.50	6.1
~83[1]	none evident	94	23.1	boulder	sand	57	—	riffle	0.20	10.4
~50[1]	neurulation	88	24.4	boulder	sand	127	—	riffle	0.20	10.4
~150[1]	none evident	88	24.4	boulder	sand	115	—	riffle	0.50	8.2
3[2]	hatched	85	24.4	boulder	sand	34	—	riffle	0.50	8.2
11[2]	hatched	85	24.4	boulder	sand	66	—	riffle	0.33	6.6
0[2]	hatched	94	24.4	boulder	gravel	269	—	riffle		

TABLE 2. Clutch sizes and ova diameters of *Atelopus*. — indicates data were not available.

Species	N	Mean clutch size (SD)	Mean ovum diameter (mm)	Method of determination	Source
A. carbonerensis	1	279	1.5	Dissection	La Marca 1984
A. chiriquiensis	1	364	2.05	Oviposited in captivity	Lindquist and Swihart 1997
A. chiriquiensis	14	370 (108)	—	Dissection	UMMZ[1] 147970–72, 147974–79, 14985, 14987
A. cruciger	1	271	1.5–1.6	Oviposited in captivity	Mebs 1980
A. flavescens	1	—	1.5–1.7	Field observation	Lescure 1981
A. franciscus	>1	~250	—	Field observation	Boistel et al. 2005
A. gracilis	1	350	0.8	Dissection	McDiarmid 1971
A. ignescens	1	372	1.3	Dissection	McDiarmid 1971
A. muisca	1	69	~2.0	Field observation	Rueda-Almonacid and Hoyos 1991
A. sernai	1	220	—	Dissection	Ruíz-Carranza and Osorno-Muñoz 1994
A. subornatus	1	189	1.8–2.2	Dissection	Lynch 1986
A. varius	1	910	1.0	Dissection	McDiarmid 1971
A. varius	1	—	1.6	Oviposited in captivity	Starrett 1967
A. varius	3	723 (26)	—	Dissection	UMMZ[1] 147973, 147980, 147988
A. zeteki	9	370 (137)	1.8	Field observation	This study

[1]University of Michigan Museum of Zoology

were heard calling at the forest edge, approximately 50 m upslope of the stream, and in damp wooded ditches that extended up into the adjacent clearing. No females were observed on that date, but on 12 December, 10 amplectant pairs were found by the stream (K. Zippel, pers. comm.). Hundreds of metamorphs were observed along the stream on 27 April 2002 (K. Zippel, pers. comm.). Oviposition in *A. chiriquensis*, another Panamanian species, probably occurs during the dry season as amplectant pairs were collected in February (Lindquist and Swihart 1997). Egg masses of *A. franciscus* from French Guyana were found in late April or early May (Boistel et al. 2005). In the same country, a clutch of *A. flavescens* eggs was found in July (Lescure 1981). In late October, a clutch of *A. muisca* was reported in Colombia (Rueda-Almonacid and Hoyos 1991). In *A. varius* in Costa Rica, breeding is estimated to begin in October and continue into early December (Crump 1988). These examples demonstrate the tremendous variation in timing of oviposition within this genus, which may be related to climatic differences between regions.

To our knowledge no clutches of *A. zeteki* have been previously reported, but descriptions of eggs and oviposition sites exist for other *Atelopus* species (Table 2). There appears to be much intraspecific variation in *Atelopus* clutch sizes. Fourteen clutches of *A. chiriquiensis* ranged from 170–603 eggs. We found that five clutches of *A. zeteki* ranged in size from 202–623 eggs. There is also interspecific variation in *Atelopus* ranging from 69 eggs in one clutch of *A. muisca* (Rueda-Almonacid and Hoyos 1991) to one of *A. varius* containing 910 eggs (McDiarmid 1971). In addition, ovum diameter varies widely in the genus, with 0.8 mm for *A. gracilis* (McDiarmid 1971) to 2.2 mm for *A. subornatus* (Lynch 1986). Ovum diameter in *A. zeteki* averaged 1.8 mm.

Duration of embryonic development has not been previously reported for *A. zeteki*. The duration of 7–11 days at 22°C reported here is comparable to the short periods described for other species of *Atelopus*. In the laboratory, eggs of *A. cruciger* hatched in three to four days at 20°C (Mebs 1980). Embryos of *A. varius* took six days to hatch in captivity (Starrett 1967), although no water temperature data were given. It appears from these limited data that the embryonic period in *Atelopus* may be relatively short.

Within our sampled reach, *A. zeteki* oviposited in wider stream sections, along shallow margins, and in fast water habitats with slightly lower canopy closure. In our study area, all clutches were attached to rocky substrates and 83% were attached to larger substrates, boulders, and bedrock. As eggs are laid during the transition between wet and dry seasons, selection of larger substrates for oviposition may reduce the risk of eggs being washed downstream in late rainy season storms, particularly in relatively confined channels such as the one in which the clutches were located. Eggs in four clutches were hatching when found. In each instance, as the rock was turned over, larvae were unable to adhere to the rock, indicating that the ventral sucking disc (Starrett 1967) characteristic of *Atelopus* either had not yet developed or does not function at hatching. Larvae slid from the remnants of the egg mass into the substrate below. It is notable that the larvae were similar in color to sand in the study area, which was the predominant substrate surrounding all but three of the clutches.

Females may select oviposition sites due to several factors including microhabitat characteristics, relative predation risk, and proximity to calling males. Although we searched 200 m of stream,

16 of 18 clutches were found within an average of 1.1 m of another clutch. Three pairs of these clutches, each pair at different development stages, were attached within 12 cm of each other on the underside of a boulder. This distribution of egg masses suggests that important locations for oviposition may be present along the stream and that communal oviposition occurs in *A. zeteki*. Communal oviposition has not been previously reported for any *Atelopus*. Communal oviposition occurs when the benefits of communal reproduction outweigh the losses to individual reproduction, females have limited clutch sizes, and suitable oviposition sites are uncommon (Robertson et al. 1998). Communal oviposition sites of *A. zeteki* may increase an individual's fitness by reducing the predation risk for a single clutch of eggs and distributing the risk among multiple clutches. The number of suitable locations for egg-laying in the vicinity of the oviposition sites reported here for *A. zeteki* is not known. However, the locations used may represent sites that are relatively stable from high flow events, during the breeding period, within those streams.

LITERATURE CITED

BOISTEL, R., S. GROSJEAN, AND S. LÖTTERS. 2005. Tadpole of *Atelopus franciscus* from French Guyana, with comments on other larvae of the genus (Anura: Bufonidae). J. Herpetol. 39:148–153.

CRUMP, M. 1988. Aggression in harlequin frogs: male-male competition and a possible conflict of interest between the sexes. Anim. Behav. 36:1064–1077.

DUNN, E. R. 1933. Amphibians and reptiles from El Valle de Anton, Panama. Occas. Pap. Boston Soc. Nat. Hist. 8:65–69.

FROST, D. R. 2004. Amphibian Species of the World: An Online Reference. World Wide Web. <http://research.amnh.org/herpetology/amphibia/index.php>. Accessed 2005 16 August.

GOSNER, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica 16:183–190.

IUCN, CONSERVATION INTERNATIONAL, AND NATURESERVE. 2004. Global Amphibian Assessment. <www.globalamphibians.org.>. Downloaded 16 March 2005.

LA MARCA, E. 1984. Longevity in the Venezuelan yellow frog (*Atelopus oxyrhynchus carbonerensis* (Anura: Bufonidae). Trans. Kansas Acad. Sci. 87:66–67.

LESCURE, J. 1981. Contribution à le'étude des Amphibiens de Guyane fançaise IX. Le têtard gastromyzophore d'*Atelopus flavescens* Duméril et Bibron (Anura, Bufonidae). Amphibia-Reptilia 2:209–215.

LINDQUIST, E. D., AND D. W. SWIHART. 1997. *Atelopus chiriquiensis* (Chiriqui harlequin frog). Mating behavior and egg-laying. Herpetol. Rev. 28:145–146.

LÖTTERS, S. 1996. The Neotropical Toad Genus *Atelopus*. Köln, Germany, M. Vences and F. Glaw Verlags GbR. 143 pp.

_____, E. LA MARCA, S. STUART, R. GAGLIARDO, AND M. VEITH. 2004. A new dimension of current biodiversity loss? Herpetotropicos 1:29–31.

LYNCH, J. D. 1986. Notes on the reproductive biology of *Atelopus subornatus*. J. Herpetol. 20:126–129.

McDiarmid, R. 1971. Comparative morphology and evolution of frogs of the neotropical genera *Atelopus, Dendrophryniscus, Melanophryniscus,* and *Oreophrynella.* Bulletin of the Los Angeles County Museum of Natural History 12:1–66.

Mebs, D. 1980. Zur Fortpflanzung von *Atelopus cruciger* (Amphibian: Salientia: Bufonidae). Salamandra 16:65–81.

Platts, W. S., W. F. Megahan, and G. W. Minshall. 1983. Methods for evaluating stream, riparian, and biotic conditions, U.S. Forest Service, General Technical Report INT-138. Ogden, Utah. 70 pp.

Robertson, I. C., W. G. Robertson, and B. D. Roitberg. 1998. A model of mutual tolerance and the origin of communal associations between unrelated females. J. Insect Behav. 11:265–286.

Rueda-Almonacid, J. V., and J. M. Hoyos. 1991. *Atelopus muisca,* nueva especie de anfibio (Anura: Bufonidae) para el Parque Nacional Natural Chingaza, Colombia. Trianea 4:471–480.

Ruíz-Carranza, P. M., and M. Osorno-Muñoz. 1994. Tres nuevas especies de *Atelopus* A. M. C. Dumeril and Bibron 1841 (Amphibia: Bufonidae) de la Coridllera Central de Colombia. Revista Academia Colombia de Ciencia 19:165–179.

Savage, J. M. 1972. The harlequin frogs, genus *Atelopus,* of Costa Rica and western Panama. Herpetologica 28:77–94.

————. 2002, The Amphibians and Reptiles of Costa Rica. University of Chicago Press, Chicago, Illinois. 1056 pp.

Starrett, P. 1967. Observations on the life history of frogs of the family Atelopodidae. Herpetologica 23:195–204.

Stuart, S. N., J. S. Chanson, N. A. Cox, B. E. Young, A. S. L. Rodrigues, D. L. Fischman, and R. W. Waller. 2004. Status and trends of amphiban declines and extinctions worldwide. Science 306:1783–1786.

A Synopsis of Bioacoustic Studies of Anuran Amphibians of Borneo

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We summarize information on acoustics recorded from the anuran amphibians of Borneo. Currently, 154 species of frogs and toads (Amphibia: Anura) are known from Borneo (Das 2005; Das and Haas 2005; Inger and Stuebing 2005). The five species of Ichthyophiidae known from Borneo presumably do not call. The quality of acoustic information of Bornean amphibians reported in the literature varies significantly. In this review, we scored call data from 0–5, where 0 = unknown; 1 = abbreviated, onomatopoeic or verbal description; 2 = analytical description only, no sonogram/oscillogram; 3 = sonogram/oscillogram only, no ana-

lytical description; 4 = sonogram/oscillogram and analytical description; and 5 = recording on a CD. In the context of this review, "analytical description" refers to an explicit summary of important call characters, such as fundamental frequency, dominant frequency, and call rate. The respective references cited are in chronological order. We report whether descriptions are based on extralimital samples; all other references pertain to Borneo, and where possible, the locality of recording is mentioned.

In total, the calls of 101 species of anuran amphibians (65.6%) known from Borneo are described in the literature. The list includes calls of several species that have been described exclusively from extralimital areas (including India, Nepal, Thailand, and the Malay Peninsula). At least in some cases (e.g., *Fejervarya limnocharis* and *F. cancrivora*), the extralimital calls refer to non-conspecific cryptic species. In a manuscript under preparation, we will describe the calls of three additional species: *Bufo quadriporcatus, Leptolalax maurus* and *Microhyla borneensis* (Sukumaran et al., in prep.).

Species with unknown calls include the sole Bornean representative of Bombinatoridae (*Barbourula kalimantanensis,* an endemic of Kalimantan, Indonesia); 15 species of Bufonidae; four species of Megophryidae; 12 species of Microhylidae; 12 species of Ranidae; and nine species of Rhacophoridae. A number of familiar species from the family Ranidae have unknown calls, or have calls inadequately described in the literature. This may be due to the logistical difficulty in getting reliable recordings due to either calling behavior (such as short, sporadic calls; call shyness; or long periods between calls) or environment (e.g., high ambient noise levels in the stream habitat characteristic of many such ranids). In addition, males of some members of the genus *Limnonectes* lack vocal sacs, resulting in their characterization in the past as 'voiceless frogs' (e.g., Emerson and Inger 1992; Emerson and Berrigan 1993; Emerson et al. 1993; Emerson and Voris 1992). However, further observations have since established that females of some of these 'voiceless frogs' do indeed vocalize (see, for instance, Emerson 1992; Inger and Stuebing 2005; Matsui 1995).

Even when call descriptions are available, these may be in an abbreviated form (descriptive or onomatopoeic), lacking sonograms or oscillograms, and thereby not available for analysis. When descriptive accounts of calls are excluded, only 75 species (48.7% of the fauna) of Bornean frog calls have been analyzed. In many cases, no vouchers are listed, sometimes making identification of the species concerned uncertain.

LITERATURE CITED

Alcala, A. C. 1962. Breeding behavior and early development of frogs of Negros, Philippines Islands. Copeia 1962:679–726.

————, G. Joermann, and J. Brzoska. 1986. Mating calls of certain Philippine anurans (Microhylidae, Ranidae). Silliman J. 33(1–4):31–44.

Arak, A. 1984. Sex and song in Malaysian frogs and toads. Malayan Natural. August 1984:20–24.