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Vocalizations of Eight Species of *Atelopus* (Anura: Bufonidae) With Comments on Communication in the Genus

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Vocalizations of frogs of the genus *Atelopus* include three discrete types of signals: pulsed calls, pure tone calls, and short calls. Repertoire composition is conservative across species. Repertoires of most species whose calls have been recorded contain two or three of these identifiable call types. Within a call type, details of call structure are very similar across species. This apparent lack of divergence in calls may be related to the rarity of sympatry among species of *Atelopus* and to the relative importance of visual communication in their social interactions.

COMMUNICATION in frogs of the genus *Atelopus* has been little studied despite several unique features of their biology that make them an important comparative system in light of the extensive work on other species of anurans (Littlejohn, 1977; Wells, 1977; Gerhardt, 1988). First, the auditory system of *Atelopus* is highly modified, and most species lack external and middle ears (McDiarmid, 1971). Second, in contrast to most anurans, species of *Atelopus* are diurnal and often brightly colored, and visual communication plays an important role in the social behavior of at least some species (Jaslow, 1979; Crump, 1988). Finally, recent behavioral studies by Crump (1988) indicate that in at least one species (Fig. 1), vocalizations primarily mediate male-male interactions and not mate attraction as is the case in most anurans.

Detailed information on vocalizations of *Atelopus* has been reported for only four species (Jaslow, 1979; Lescure, 1981; Asquith and Altig, 1987), and laryngeal morphology has been examined in three species (Martin, 1972). From our fieldwork, recordings made by colleagues, and a review of the tape archives of the National Museum of Natural History (USNM), the American Museum of Natural History (AMNH), and the Museum of Natural History, University of Kansas (KU), we have analyzed recordings of the calls of eight species of *Atelopus*, including seven species for which calls have not been reported previously. These species include *A. cruciger*, *A. minutulus*, *A. nicefori*, *A. senex*, *A. spumarius* (two populations), *A. varius* (two populations), *A. zeteki*, and *A.* sp. Our purposes are: 1) to summarize the available information on calls of *Atelopus*; and 2) to ask what this information suggests about call evolution in *Atelopus* by comparing the structure and behavioral context, where available, of calls of these species with calls of other species reported in the literature.

METHODS

Calls were analyzed using a Kay Digital Sona-Graph 7800, a Data 6000 Waveform Analyzer with a model 610 plug-in digitizer, and a Multigon Uniscan II real-time analyzer. Call frequencies were measured from waveform and Fourier transform analyses; pulse rates and call lengths were measured from waveform analyses or from wide-band audiospectrograms. Call rates were measured from the real-time analyzer screen or with a stopwatch directly from the tapes. Original tapes of some species and copies of all tapes are on file in the tape archive, Division of Amphibians and Reptiles, USNM; original tapes of other species are on file as indicated below.

Few field recordings of *Atelopus* are available, and therefore some of the recordings utilized in this and other studies (Asquith and Altig, 1987; Jaslow, 1979; Lescure, 1981) were made from animals in captivity. We tested the potential for distortion of calls from animals calling from plastic bags by analyzing recordings of a single male of *Hyla koechlini* Duellman and Trueb calling in and out of a bag (this species has a pulsed call somewhat similar in structure to calls of *Atelopus*); our analyses showed no discernible difference between the two recordings. We also carefully inspected laboratory recordings for evidence of reverberation or smearing of the call waveform. Calls with waveforms showing evidence of degradation were eliminated from the temporal analyses.

Fig. 1. Male *Atelopus varius* from a population along the Rio Lagarto, 3 km SSW Santa Elena, Puntarenas Province, Costa Rica. Males in this population apparently use the pulsed call to communicate with other males and rely on visual cues to locate mates (Crump, 1988). Photo courtesy of Martha L. Crump.

We use the following abbreviations in reporting call data: call length (cl); pulse rate (pr); number of pulses (pn); dominant frequency (df); and frequency modulation (fm). All snout–vent length (SVL) measurements are in millimeters. Institutional abbreviations follow Leviton et al. (1985).

Materials

Frogs of the genus *Atelopus* often are conspicuous members of Neotropical anuran faunas in evergreen wet forest habitats, especially at elevations between 800 and 2000 m from Costa Rica south to Bolivia and in the Guianas and northern Brazil. These diurnal, slow-moving frogs are usually brightly colored and frequently concentrate along small to moderate-sized streams, in which they breed. In spite of their conspicuousness and diversity (Frost [1985] listed 43 species), relatively little is known about their reproductive ecology and behavior. Male size, habitat, and general range of the nine species studied in this work are reported in Table 1.

Atelopus cruciger (Lichtenstein and Martens).—This species is relatively common along several of the streams that drain the wet forests of Parque Nacional Henri Pittier, which includes the biological research station of Rancho Grande in northern Venezuela. Although *Atelopus* is poorly known as a group, *A. cruciger* is an exception primarily because of its relative abundance and the published observations on its life history (Sexton, 1958) and larval development (Mebs, 1980). Even though Sexton (1958) reported that males of this species call, no literature on vocalizations of *A. cruciger* exists.

Several calling males of *A. cruciger* (SVL about 30) were located by RWM along a rocky stream about 1 km south of Cuyagua, Estado Aragua, Venezuela, on 19 Dec. 1976. About 12 males were seen in a 20 m section of the shoreline. Seven single males and an amplexing pair were collected and transported to Caracas where they were put into a planted terrarium and observed. Some of the males resumed calling. At least three distinct types of calls given by captive male *A. cruciger* were recorded in the laboratory: a pulsed call, a pure tone call, and a short call (temperature information not available).

Atelopus minutulus Ruiz-Carranza, Hernandez-Camacho and Ardila.—This small species was recently described from specimens taken at a single site in wet forest at 1560 m near Vereda de Portachuelo (vic. Manzanares), Departamento de Meta, Colombia. W. Lamar located males (SVL $\bar{x} = 19.8$, n = 25) calling from rocks along the edge of a small stream at 1640 m between 1530 and 1700 h on 8 July 1980. He recorded

TABLE 1. SPECIES OF *Atelopus* FOR WHICH CALL DATA ARE REPORTED IN THIS STUDY. Male SVL, habitats and distributions, and sources of information are indicated.

Species/SVL (mm)	General distribution	Source
Atelopus cruciger 28–33	cloud forests, coastal range of northern Venezuela	Sexton, 1958
Atelopus minutulus 17–20	cloud forests, eastern Andes, Meta, Colombia	Ruiz-Carranza et al., 1988; Lamar, pers. comm.
Atelopus nicefori 17.5–22.5	montane wet forests, near Caicedo, Antioquia, Colombia	Rivero, 1963; Ruiz-Carranza et al., 1988
Atelopus spumarius 23–29	Amazonian lowlands, Peru, Ecuador, northern Brazil and Guianas	Peters, 1973; Lescure, 1973, 1981
Atelopus senex 28–32	montane wet forests, central and southern Costa Rica	Savage, 1972
Atelopus varius 27–41	wet forests, Costa Rica, Panama and northern Colombia	Savage, 1972
Atelopus zeteki 34–43	wet forests, Valle de Anton area of western Panama	Dunn, 1933; This study
Atelopus sp. 24–29	Caribbean lowlands, eastern Panama	Myers, pers. comm.

at least three call types from individuals in a plastic bag (temperature information not available).

Atelopus nicefori Rivero.—This small species (male holotype measured 19 SVL) has been reported from two localities, at 1800 and 2670 m, near Caicedo, Antioquía, Colombia (Rivero, 1963; Rivero and Serna, 1985). Frogs at the higher elevation were found in wet forest near the mouth of a small stream. Five calls were recorded by PRC from a male *A. nicefori* (ICN 1304, SVL 21.3) found in amplexus with a female during the day on 30 April 1972, at "La Nevera," Vereda El Chuscal, Departamento Antioquía, Colombia. This locality is in a residual patch of cloud forest at 2585 m elevation on the western slope of the Western Andes. The pair was taken with several other individual males and females along a small, clear creek; water temperature was 10.5 C and air temperature 12 C.

Atelopus spumarius spumarius Cope and A. s. hoogmoedi Lescure.—*Atelopus spumarius*, a member of the *flavescens* group (McDiarmid, 1971; Lescure, 1981), is a wide-ranging species known from several localities in eastern Ecuador and Peru, the northern Amazon Basin of Brazil, and the Guianan area. Like other species in the genus, it is diurnal and found in primary wet forests. Male size varies among populations. A series of short calls was recorded by RBC from captive specimens (USNM 269068–269069, 19–21 SVL) of *A. spumarius spumarius* collected at 640 m on the Rio Tambopata, Departamento Madre de Dios, Peru (temperature information not available). Thirteen calls of a single male (KU 129958, 29.4 SVL) referred to *A. s. hoogmoedi* (Lescure, 1981) from the SUDAM Floral Reserve, 74 km SE Satarem, Estado Pará, Brasil, were recorded by Martha Crump on 5 July 1970; temperature 27 C (KU tape 989, Reel 88).

Atelopus varius group.—*Atelopus chiriquiensis, A. senex, A. varius* (an extremely variable species), and *A. zeteki* (considered a subspecies of *varius* by many authors) are closely related members of a Middle American species group reviewed by Savage (1972). These forms are diurnal and usually found near fast-moving, small streams in wet evergreen forests from near sea level to above 2150 m. In spite of their having been relatively well studied (Savage, 1972; Crump, 1988) the only data on vocalization in these species are the single sound spectrogram of *A. varius* from Costa Rica (Starrett, 1967) and the more complete work on *A. chiriquiensis* from Panama (Jaslow, 1979).

Atelopus senex Taylor.—Three recordings were made by W. E. Duellman between 2320 and 2345 on 1 April 1966, temperature 17.7 C, on the south fork of the Rio Las Vueltas, Heredia Province, Costa Rica. Tape speed was irregular on all three recordings. Limited analyses were

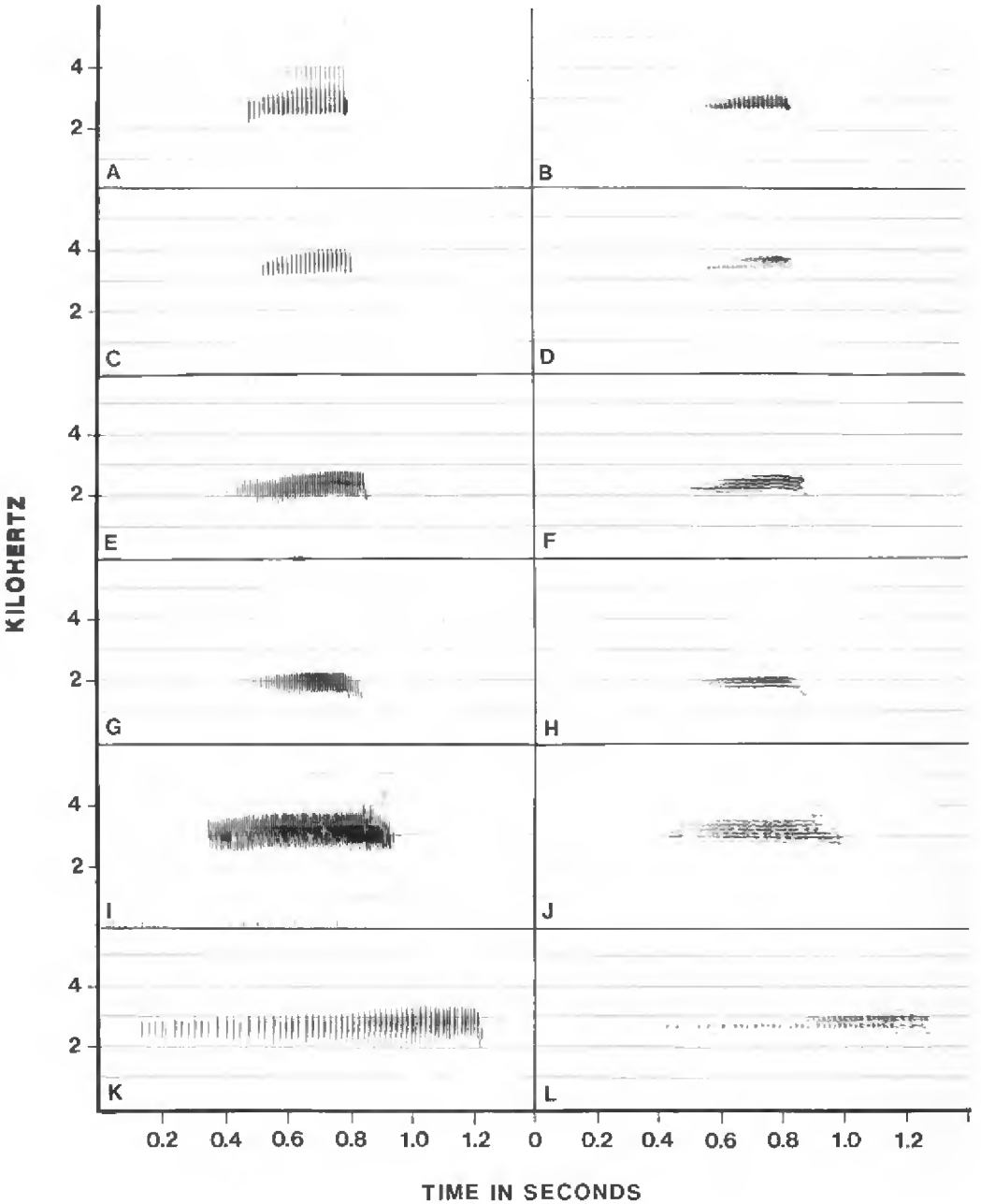

Fig. 2. Audiospectrograms of the pulsed call of six species of *Atelopus*. For each species, the left side display is with a wide-band filter (300 Hz) and the right side is with a narrow-band filter (45 Hz). (A–B) *A. nicefori*; (C–D) *A. minutulus*; (E–F) *A. varius*; (G–H) *A. zeteki*; (I–J) *A. cruciger*; (K–L) *A. spumarius*.

made of the last recording, in which pitch fluctuation is least apparent (KU tape 812, Reel 88).

Atelopus varius (Lichtenstein and Martens).—Individuals of this species were found by APJ on clean boulders, gravel banks, and the forest floor adjacent to three small streams between 670 and 790 m elevation, 2–6.4 km W of Alto Piedra school, N of Santa Fe, Veraguas Province, Panama. Males were widely dispersed along the

streams on 9 Sept. 1978 at a density of about 4–6 individuals along 30–40 m sections of the shoreline; none was seen in the adjacent forest. One amplexing pair also was found at this time. Only non-calling males were found in July 1983 at this site. Recordings of two males (USNM 292533, 36.6 SVL; 292540, 37.1 SVL) were made in the field (temperature information not available).

Atelopus zeteki Dunn.—This species was observed by APJ near a sawmill 12 km NE El Copé, Cocle Province, Panama. This locality is in cloud forest at 600–800 m near the continental divide and is farther west than previously reported populations from near El Valle (Dunn, 1933; Miller, 1987). Individuals were active in April and Oct. 1977, Jan. 1978, and March 1979. Males called in April, Oct., and March, whenever the forest was wet from recent rain. Frogs were common adjacent to the steams and in the forest. These golden frogs often were seen sitting on plant-covered boulders, logs, and roots or found walking on litter in the forest. At night, individuals were found exposed on broad leaves up to 1 m above ground. Several calls were recorded from one male in the field on 20 April (air temperature 21.8 C) and from an amplexing male in a terrarium crowded with males and females (air temperature 27.8 C). All frogs of this protected species were released in the field.

Atelopus sp.—This form is widespread in the Caribbean lowlands of eastern Panama. We refrain from assigning these specimens from Sasardí, San Blas Province, Panama, to a described species and recognize that they may represent an undescribed species in the *varius* complex (Savage, 1972; C. W. Myers, pers. comm.). Several short calls were recorded between 5 and 7 Feb. 1967 by C. W. Myers from an individual male in a bag containing 16 specimens of this species (3 adult males [KU 115923, 115925, 115928] measured 24.0, 26.1, and 29.2 SVL); air temperature was 32 C (KU tape 815, Reel 88).

Results

Atelopus cruciger.—The first of three call types recorded from the captive *A. cruciger* is a series of pulses. Frequency modulation is variable in the calls recorded, but in most the df rises slightly toward the end of the call, then falls slightly; some calls show no fm. Some calls are broken into two or three shorter notes. Amplitude increases gradually during most of the call and decreases slightly at the end (Fig. 2I–J; Fig. 5B; Table 2). The second type of call is a pure tone that rises in frequency. Calls are partially pulsed, but pulsation is irregular and variable within and between calls (Fig. 3B; Table 3).

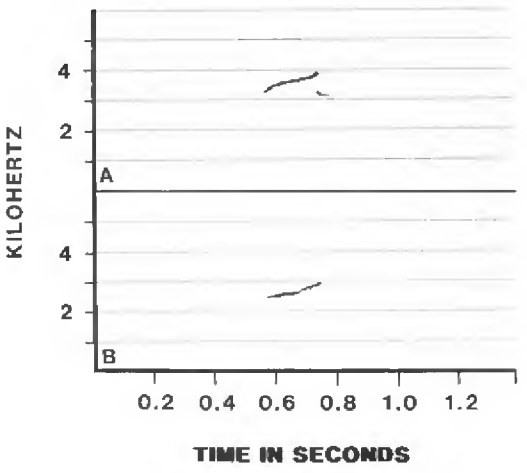

Fig. 3. Audiospectrograms of the pure tone call of *Atelopus minutulus* (A) and *A. cruciger* (B) with a narrow-band filter (45 Hz).

The third type is a short, quiet, partially pulsed call, descending in frequency. These calls were given by apparently non-interacting captive individuals, by males in a bag with other males, and by a male in amplexus with a female (Fig. 4I–J; Table 3).

In addition to these three distinct call types, a series of variable calls was given by one male before a series of pulsed calls. These calls are intermediate in length and degree of pulsation between the first and third types, and consist either of a short, non-frequency modulated series of pulses, or of a brief, unpulsed segment followed by a series of pulses.

Atelopus minutulus.—At least three types of calls were recorded by Lamar from captive males of this small species. The first type (Fig. 2C–D; Fig. 5G; Table 2) consists of a series of pulses. Dominant frequency rises within the call, usually dropping slightly at the end. Amplitude increases gradually throughout the call and usually decreases slightly at the end (amplitude changes roughly parallel frequency changes). Pulse rate also increases slightly (2–9%) within calls.

TABLE 2. PHYSICAL PARAMETERS OF PULSED CALL TYPES FROM SEVEN SPECIES OF *Atelopus*. Values are given as means and ranges. Sample size is given as total number of calls sampled/total number of frogs sampled.

	cruciger	*minutulus*	*nicefori*	*spumarius hoogmoedi*	*senex*	*varius*	*zeteki* male-1	*zeteki* male-2
Call length (msec)	690 (620–770)	282 (227–381)	350 (330–370)	1120 (1060–1240)	—	403 (373–460)	425 (413–431)	344 (297–363)
Pulses per call	91.2 (84–99)	18 (14–21)	22.8 (21–24)	61.6 (57–71)	32.5 (30–34)	47.7 (43–56)	49.0 (48–50)	49.0 (42–52)
Pulses per second	131.9 (128–140)	64.8 (59.5–67.9)	65.0 (63.9–65.7)	43.1/74.0* (39.3–47.7/70.0–81.7)	—	120.1 (119–123)	118.2 (115–119)	145.2 (143–146)
Dominant frequency (Hz) start of call	2750 (2650–2990)	3182 (2950–3380)	2645 (2630–2670)	2708 (2670–2750)	—	2350 (2210–2480)	1780 (1620–1950)	1820 (1680–1915)
Peak near end of call	3065 (2990–3170)	3387 (3165–3690)	2871 —	2956 (2870–3000)	—	2468 (2410–2520)	2007 (1915–2050)	1985 (1915–2225)
Frequency modulation (Hz)	+281 (+90–+480)	+205 (+80–+310)	+226 (+200–+240)	+248 (+120–+300)	—	+120 (+10–+230)	+231 (+40–+430)	+165 (+40–+390)
Sample size	10/2	9/>1	5/1	10/1	6/1	10/2	5/1	5/1

* Pulse rates and ranges for the start and end of calls, respectively.

The second type of call (Fig. 3A; Table 3) is a pure tone that rises in frequency, usually followed immediately by a short note with a slightly lower frequency. The frequency in some calls of one male increased and then dropped gradually (rather than abruptly) to the final note.

The third type (Fig. 4C–D; Table 4) is short, quiet, descending in frequency, and irregularly partially pulsed.

As in *A. cruciger*, some variable calls were produced that had no consistent characteristics and were difficult to categorize. Most were somewhat similar to the pure tone calls (above) but with irregular fm; often these calls were broken into shorter notes.

Atelopus nicefori.—This call is a series of regular pulses. The df rises during the call; amplitude increases during the first third of the call and remains the same for the rest of the call. Pulse rate also increases very slightly within each call (in species from which an increase in pr was detectable but slight, we report average pr for the entire call). The last pulse is longer and slightly lower in frequency than the pulses immediately preceding it (Fig. 2A–B; Fig. 5F; Table 2).

Atelopus spumarius spumarius and A. s. hoogmoedi.—The short, quiet calls (Fig. 4A–B; Table 4) recorded from captive *A. s. spumarius* collected on the Rio Tambopata are partially pulsed, and some calls are slightly frequency modulated up or down. Calls were given singly or in groups of two or three in close succession.

The call of *A. s. hoogmoedi* from Para, Brasil is a series of pulses; the pr increases from the beginning to the end of the call. The df rises gradually throughout the call, falling slightly at the end in some calls. Amplitude increases gradually to a point near the end of the call, then decreases (Fig. 2K–L; Fig. 5A; Table 2).

Atelopus senex.—The recordings of this species consist of six calls from a single male (KU 103541, 27.4 mm SVL). Accurate frequency and temporal data are not retrievable, but waveform analyses show that the call is a series of pulses (Fig. 5E; Table 2) that increase in amplitude to a point ⅔ to ¾ way through the call, then decrease. Pulses in most calls are strongly partially pulsed.

Atelopus varius.—The first type of call is a series of pulses. Dominant frequency rises gradually

through the call and decreases slightly at the end. Amplitude increases gradually through the call, paralleling the frequency increase, and drops at the end (Fig. 2E–F; Table 2). The last pulse in some calls is longer than the preceding pulse.

A second series of calls (similar to those recorded by Myers for *Atelopus* sp.) was recorded from one male in a plastic bag with several other males. These calls are short, quiet, and irregularly partially pulsed. Dominant frequency usually decreases and then increases within the call; for three of 10 calls frequency only decreases (Fig. 4E–F; Fig. 5C; Table 4).

Atelopus zeteki.—The first of two recorded call types (Fig. 2G–H; Table 2) is a series of pulses. Values for each male are given separately because of temperature differences. Dominant frequency increases throughout the call, although the final pulse is slightly lower and usually longer than the preceding pulses. Amplitude increases gradually, decreasing slightly in the last pulse (Fig. 5D). The pr increases slightly (2–6%) toward the end of the call. This call was recorded from both the amplectant captive male and the male in the field. Surprisingly, the terrarium recording showed very little degradation, unlike a similar recording of *A. varius* (not reported). Three of five calls of this male showed no degradation, and two showed only very slight smearing that did not obscure the temporal structure of the call. Differences in pr, cl, and df may reflect intrapopulational variation or variation due to temperature or both (male 1 recorded at 21.8 C; male 2 at 27.8 C).

TABLE 3. PHYSICAL PARAMETERS OF PURE TONE CALL TYPES FROM TWO SPECIES OF *ATELOPUS*. Values are given as means and ranges. Sample size is given as total number of calls sampled/total number of frogs sampled.

	cruciger	*minutulus*
Call length (msec)	232 (180–290)	244 (189–297)
Dominant frequency (Hz)		
Start of call	2480 (2400–2550)	3068 (2770–3275)
End of call	2860 (2810–2870)	3565 (3275–3780)
Final note	—	3034 (2835–3150)
Frequency modulation (Hz)	+370 (+320–+470)	+497 (+375–+630)
Sample size	5/1	10/≥2

The second type of call (Fig. 4G–H; Table 4) is short, quiet, and frequency modulated downward. Unlike similar calls of the other species reported, these calls were completely unpulsed. Calls were given by the captive male while in

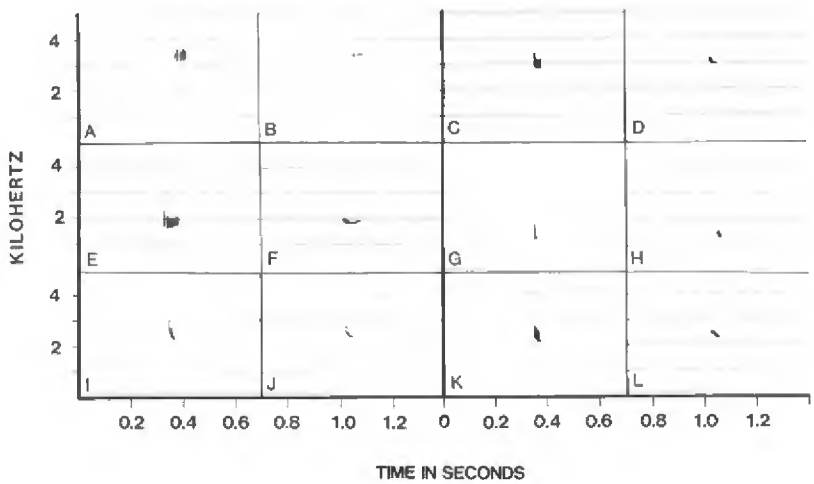

Fig. 4. Audiospectrograms of the short calls of six species of *Atelopus*. For each species, the left side display is with a wide-band filter (300 Hz) and the right side is with a narrow-band filter (45 Hz). (A–B) *A. spumarius*; (C–D) *A. minutulus*; (E–F) *A. varius*; (G–H) *A. zeteki*; (1–J) *A. cruciger*; (K–L) *Atelopus* sp.

TABLE 4. PHYSICAL PARAMETERS OF SHORT CALL TYPES FROM SIX SPECIES OF *ATELOPUS*. Values are given as means and ranges. Sample size is given as total number of calls sampled/total number of frogs sampled.

	cruciger	*minutulus*	*spumarius spumarius*	*varius*	*zeteki*	*sp.*
Call length (msec)	48 (30–80)	28 (22–37)	60 (30–100)	61 (34–70)	30 (26–33)	25 (20–34)
Dominant frequency (Hz)						
Start of call	2575 (2390–2970)	3164 (3125–3435)	3380 (2980–3430)	1965 (1920–2010)	1510 —	2585 (2510–2640)
Low point of call	— —	— —	— —	1823 (1780–1930)	— —	— —
End of call	2385 (2310–2630)	2975 (2815–3125)	3370 (3320–3430)	1856 (1750–1920)	1385 —	2460 (2350–2580)
Frequency modulation (Hz)	−192 (−70–−480)	−213 (−155–−310)	−10 (−80–+40)	−160/+51* (−100–−260/0–+120)	−125 —	−120 (0–−290)
Sample size	12/≥1	8/≥1	10/1–3	11/1	5/1	10/1

* Frequency modulation means and ranges for the descending and ascending portions of calls, respectively.

amplexus with a female and in the presence of other males.

Atelopus sp.—Calls are short, quiet, and given one at a time or twice in rapid succession. Some calls are frequency modulated downward and some are partially pulsed (Fig. 4K–L; Table 4).

TAXONOMIC NOTE

We have attempted to evaluate the variation in calls from across the range of the widespread species *A. spumarius*. Lescure (1981) discussed geographic variation in color pattern in the *flavescens* group and presented calls of three subspecies of *A. spumarius (barbotini, hoogmoedi,* and *spumarius)*. Asquith and Altig (1987) published a sonagram of the call of *A. s. spumarius* from near Nauta, Departamento Loreto, Peru, and noted that the df, call duration, and number of pulses in the call differed from those of the call of *A. s. spumarius* reported by Lescure (1981) from a specimen from Yubineto, Departamento Loreto, Peru. Also, comparison of call characteristics of *A. s. hoogmodei* from French Guiana (Lescure, 1981) and from Estado Pará, Brasil (this report) indicate differences in pn and pr.

The range of values of pr, pn, and df for the calls of *A. spumarius* from five populations from a geographically widespread area encompasses the range of values of pr and pn for *A. flavescens* and *A. franciscus*, the other two members of the *flavescens* group for which calls are available. Little or no information is available on intraspecific variation in call characteristics from within a single population, or on call function in this group. However, the relatively high degree of variation of call characteristics within *A. spumarius*, coupled with the distribution of this species from the Guianas across the northern Amazon Basin to the lower eastern slopes of the Andes, suggest that *A. spumarius* may comprise a complex of species.

A similar pattern of geographic variation and probable speciation may be present in populations of *Atelopus varius*. We are certain that some of the Panamanian populations referred to *A. varius* by Savage (1972) will be shown to represent distinct species. The reports (Fuhrman et al., 1969; Kim et al., 1975; Brown et al., 1977) of distinctive toxins in the skin of *Atelopus* from different populations in Panama and Costa Rica support our contention that *A. zeteki* is distinct from *A. varius*, and we treat it accordingly.

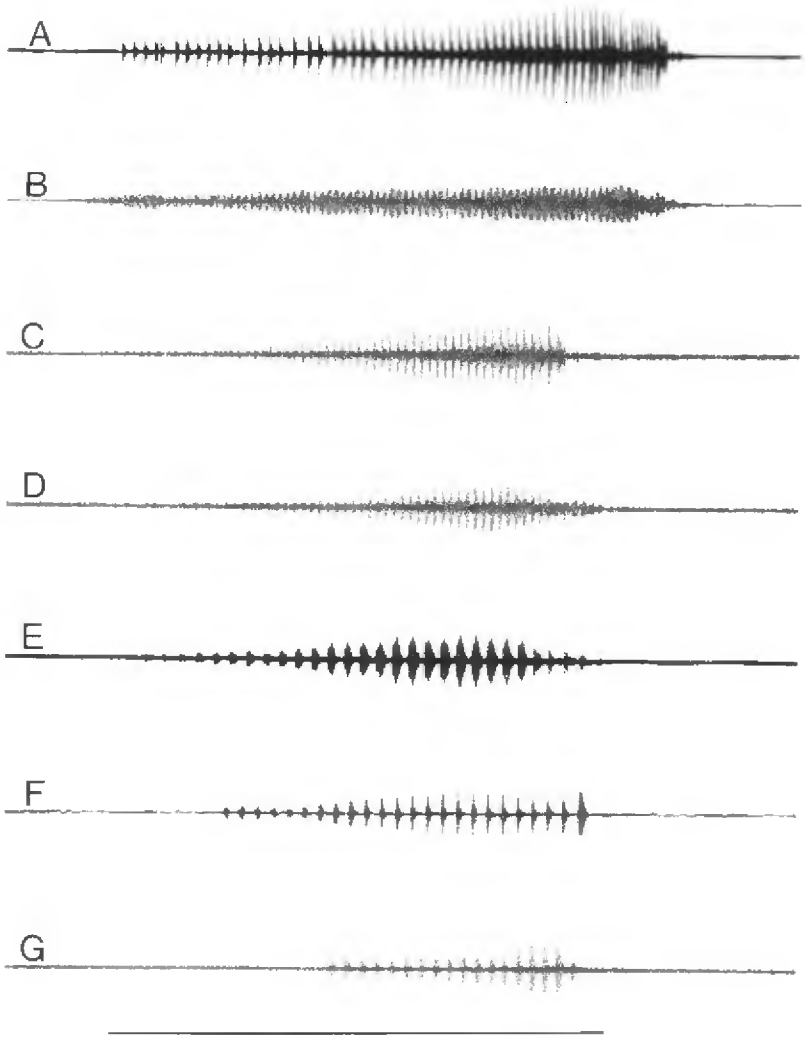

Fig. 5. Waveforms of pulsed calls of seven species of *Atelopus*: (A) *A. spumarius*; (B) *A. cruciger*; (C) *A. varius*; (D) *A. zeteki*; (E) *A. senex*; (F) *A. nicefori*; and (G) *A. minutulus*. The line at bottom represents 1.0 sec for tracing in (A) and 0.5 sec for tracings in (B–G).

Discussion

Although McDiarmid (1971) suggested (based on the loss of a tympanum and middle ear in many species) that some species of *Atelopus* were losing the ability to use acoustic signals in their reproductive behavior, the species discussed here are characterized by a repertoire of call types. In fact, one of the most striking results of our survey of *Atelopus* calls is the occurrence of the same set of fixed call types across species. Furthermore, within a given call type, calls of different species are very similar in structure.

Pulsed call.—These calls (termed "buzz" calls by Jaslow [1979]) have been reported for 10 species (Table 5). Although pr and df vary among species, the overall structure of the pulsed call remains the same. Dominant frequency increases gradually through the call, and usually falls slightly at the end. In most of the species for which pr has been measured, pr increases from the beginning to the end of the call (the magnitude of the change, however, varies among species, and no pr change was observed in calls of *A. cruciger* or *A. varius*). Amplitude changes within pulsed calls also are characteristic. Calls

TABLE 5. REPORTED CALL TYPES OF SPECIES OF *Atelopus*.

Species	Call types			Source
	Pulsed	Pure tone	Short	
A. chiriquensis	X	X	X	Jaslow, 1979
A. cruciger	X	X	X	This study
A. flavescens	X			Lescure, 1981
A. franciscus	X			Lescure, 1981
A. minutulus	X	X	X	This study
A. nicefori	X			This study
A. senex	X			This study
A. spumarius spumarius	X		X	This study; Asquith and Altig, 1987; Lescure 1981
A. spumarius barbotini	X			Lescure, 1981
A. spumarius hoogmoedi	X			This study; Lescure, 1981
A. varius	X		X	This study; Starrett, 1967
A. zeteki	X		X	This study
A. sp.			X	This study

begin quietly, gradually increase in intensity to a peak near the end of the call, then decrease or remain constant to the end. Amplitude and frequency appear usually to be coupled within the call, such that the loudest point is also the highest. In the calls in which pr changes, the changes are in the same direction as frequency and amplitude.

The observed similarity in details of structure among pulsed calls suggests that calls are produced in the same manner in these species. We do not have enough data, however, to determine with certainty whether the mechanism of amplitude modulation is the same in each species.

Pure tone calls.—These calls (termed "whistle" calls by Jaslow [1979]), have been recorded in three species (Table 5). These calls are intermediate in length between pulsed and short calls. In *A. cruciger* and *A. minutulus* this call is frequency modulated upward, while in *A. chiriquiensis* the call is not frequency modulated.

Short calls.—Short calls (termed "chirp" or "twitter" calls by previous authors) have been reported for seven species (Table 5). At least some calls of each species show frequency modulation downward or upward. Calls of five species for which waveforms have been analyzed are slightly to moderately partially pulsed, whereas calls of a sixth (*A. zeteki*) are unpulsed. In each population for which short and pulsed calls have been recorded, short calls are lower in both frequency and amplitude than pulsed calls.

Other calls.—In addition to these three identifiable call types, a number of variable calls were heard from some individuals of *A. cruciger* and *A. minutulus* (see above). It is unclear whether these calls represent a distinct call or whether they are partial or intermediate calls. The "prelude" call reported by Lescure (1981) for *A. s. barbotini* seems somewhat similar to the variable call for *A. minutulus* and to some of the variable calls of *A. cruciger* but we presently do not have enough information to determine whether or not these calls represent an identifiable call type in the repertoire of these species.

Peters (1973) reported the voice of *A. arthuri* as a "low, chicklike peep" and characteristic of other Ecuadorian *Atelopus* where known. Peters (1973) noted that an occasional male *A. arthuri* will "trill the peep slightly." Although it is tempting to suggest that these calls may be the same as the pulsed call known from other species, how these calls relate to the call types described above is unknown. Peters (1973) also mentioned that male *A. ignescens* use slow kicking and soft peeping to discourage other males from amplexing them. From a behavioral perspective this soft "peep" seems to be used in aggressive interactions associated with male-male contact (see later discussion) and may be equivalent to the short call of other species.

Behavioral context of vocalization.—Available evidence suggests that the pulsed call is an advertisement call in those *Atelopus* species reported here, functioning (at least in some species) in male-male interactions. The pulsed calls re-

ported in *A. chiriquiensis* (Jaslow, 1979) and in *A. varius* (Crump, 1988) apparently function as advertisement calls, announcing the location of one male to another. To our knowledge, no one has observed courtship and pairing in any species of *Atelopus*. Based on a single observation by Weed (reported in Jaslow, 1979), it was suggested that the pulsed call of *A. pulcher* (=*A. spumarius*) functions in female attraction. In contrast, Crump (1988) does not believe that vocalization is important in female attraction or pairing in *A. varius*. In the absence of observations of pairing and the appropriate experimental evidence, the behavioral significance (if any) of these calls in mate attraction in *Atelopus* will remain unclear.

Observations by Lescure (1981) suggest that the pulsed call in three populations of *A. spumarius*, *A. flavescens*, and *A. franciscus* may function as an advertisement call in these species as well. A pulsed call of *A. spumarius* from northeastern Peru was recorded from a single individual in a jar (Asquith and Altig, 1987). In *A. nicefori* and *A. zeteki*, pulsed calls were given by males in amplexus with females. In *A. zeteki*, pulsed calls also were recorded from a single male in the field; several other males at this site also were giving pulsed calls but were not recorded.

Available information does not permit an interpretation of the context of the pure tone calls in *A. cruciger* and *A. minutulus*. In *A. chiriquiensis* the pure tone call was given by males in aggressive encounters (Jaslow, 1979).

The short call or "contact" call has been recorded from males in proximity to other males and from males in amplexus. We assume that the "more typical" call of *A. varius* reported by Starrett (1967) was of this type. Crump (1988 and pers. comm.) has reported short calls in *A. varius* given by fighting males and recently amplexed males as the female attempted to dislodge them. We have recorded short calls from an amplexing male of *A. zeteki* and *A. cruciger*. The amplexing male *A. cruciger* increased his call rate when approached or contacted by another male. Short calls often have been recorded from males held in a collecting bag with other individuals (Table 5).

Summary.—In general, the species of *Atelopus* whose calls have been recorded are characterized by a repertoire of two or three distinct call types. The most consistent type across species is the pulsed call (Table 5). However, because the vocal behavior of most species reported here has not been studied in detail, the lack of a reported call type probably reflects inadequate sampling rather than a real absence. We expect that as more species are studied in detail, additional call types will be found in species for which only one or two types currently are known.

The evolution of call repertoires has been conservative in the *Atelopus* species for which we have call data. There is no clear a priori reason why call repertoires should be restricted to certain fixed call types. The occurrence of occasional atypical, highly variable calls in the recordings of some captive males suggests that repertoire composition is not constrained by signal production mechanisms. However, within the general range of frequency and duration characteristics of *Atelopus* calls, these three call types probably represent about the most distinctive possibilities. The distinctiveness of pulsed vs pure tone vs short calls may allow for a more immediate, unambiguous identification of the signal type (and its information content) by the receiver than would be possible with other, more intermediate call types (see Moynihan, 1970, for a discussion of possible limitations on repertoire composition).

It is unclear whether the behavioral significance of the different call types is the same in all species where they occur. Perhaps some call functions (e.g., mate attraction) have been lost in certain taxa and retained in others. It is also possible that two different call types play the same role in the communication system of different species. For example, the call given during amplexus by *A. cruciger* was the short call, whereas in *A. nicefori* it was the pulsed call.

Call structure within a given call type also has been highly conserved in *Atelopus*, although more diversity likely will be encountered as calls of more species become known. A number of factors may be related to this apparent lack of divergence in calls. First, sympatry of more than one species of *Atelopus* at a given site is rare. Second, calls in at least some species may not function in mate attraction (Crump, 1988). Thus, selection for reproductive isolation through species-specific vocalizations, as well as sexual selection acting on male calls through female choice, may be less important in *Atelopus* than in other anuran groups. Finally, visual communication may be more important than acoustic communication for some signal functions. All species of *Atelopus* are diurnally active and many have widespread color and pattern

polymorphisms suggesting that mate selection may depend more on visual than on vocal recognition (McDiarmid, 1971). In his descriptions of the breeding behavior of two Ecuadorian species (*A. arthuri* and *A. ignescens*), Peters (1973) stated that males call as they walk about searching for females during mass breeding movements but that males of these species locate mates entirely on a visual basis. Crump (1988) observed stereotyped foot-waving, an apparent visual signal used during aggressive encounters in *A. varius*. One of us (APJ) observed foot-waving in *A. varius* at Alto Piedra in Panama.

Martin's (1972) studies of cell evolution in *Bufo* demonstrate that call mechanisms and call structure are conserved within certain lineages in that genus. Conserved structural elements in calls also occur within species groups of centrolenids (McDiarmid, unpubl.), some genera of microhylids (Nelson, 1973), and within some genera and species groups of hylids (Cocroft, unpubl.). In some cases, close relatives also appear to share call repertoires (e.g., *Bufo* advertisement and release calls [Brown and Littlejohn, 1972]; advertisement and secondary call types of *Sphaenorhynchus* and some *Ololygon* [Cocroft, pers. obs.]). However, further comparative studies will be necessary in order to place these specific examples within a more general context of anuran call evolution.

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