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MATING CALLS OF THE MICROHYLINAЕ: DESCRIPTIONS AND PHYLOGENETIC AND ECOLOGICAL CONSIDERATIONS

CRAIG E. NELSON

ABSTRACT: Data from audiospectrographic analyses of mating calls are available for representatives of the New World microhylinae genera *Dermatonotus*, *Elachistocleis*, *Hypopachus*, *Gastrophryne*, *Glossostoma*, *Hamptophryne*, *Synapturanus*, *Arcovomer*, *Dasylops*, *Ctenophryne*, *Chiasmocleis*, and *Stereocyclops* and the Asiatic microhylinae genera *Glyphoglossus*, *Kaloula*, *Ramanella*, and *Microhyla*. Verbal descriptions are available for an additional American genus, *Myersiella*, and for the Asiatic genera *Uperodon*, *Kalophrynus*, *Chaperina*, and *Metaphrynella*.

Carvalho's (1954) suggested affinities among New World genera are confirmed from comparisons of mating calls for several groups: *Dermatonotus*, *Elachistocleis*, *Hypopachus*, and *Gastrophryne*; *Glossostoma* and *Dermatonotus*; *Synapturanus* and *Myersiella*; and *Stereocyclops*, *Ctenophryne*, and *Chiasmocleis*. Such intergeneric similarities in call are unusual and may reflect either an extended range of applicability of call data or relatively fine intergeneric taxonomic distinctions. However, the calls of *Hamptophryne*, *Arcovomer*, and *Dasylops* do not match Carvalho's (1954) suggested affinities.

Among forms with similar calls, those having a larger body size usually have lower dominant frequencies. Genera in which the males call from dispersed sites (terrestrial nests, land-crab burrows, or tree holes) have calls that are high-pitched short, relatively pure, single notes. They thus have the properties suggested by other authors (e.g., Marler, 1955) as minimizing locatability by predators.

THE subfamily Microhylinae of the anuran family Microhylidae includes 10 genera in the Oriental region (Parker, 1934) and 15 in the New World (from Carvalho, 1954, but combining *Elachistocleis* and

Relictivomer as suggested by Rivero, 1961, and others) or 16 if *Geobatrachus* is transferred into the family as suggested by Lynch (1971). Appreciably different schemes of affinities among these forms have been

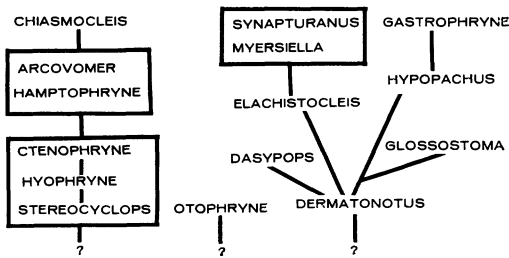


FIG. 1.—Intergeneric affinities of New World Microhylidae as suggested by Carvalho (1954). Lines indicate affinity but not evolutionary distance.

expressed. Parker (1934) regarded several species in both regions as belonging to the genus *Microhyla* whereas Carvalho (1954) distributed the New World species so treated by Parker among 4 genera. Carvalho (1954) gave explicit statements of affinity linking most of the New World genera (Fig. 1). As Carvalho had no knowledge of the calls of most of the genera, comparisons of calls provide a partial test of his suggested affinities. Heyer (1971), following the analysis by Konishi (1970), suggested correlations between calling site and mating call type for Asiatic Microhylidae. These correlations, and others suggested by Marler (1955, 1957) for animal vocalizations, can also be partially tested by analysis of differences among New World forms.

Tape recordings and audiospectrograms are available for 12 New World genera. A verbal description is available for *Myersiella*, which leaves only three monotypic genera without described calls: *Otophryne*, *Hyophryne* (known only from the type), and *Geobatrachus* (assuming it is a microhylid). There are relatively few New World species not included: some data on the call are available for all species in all New World genera for which any calls are known except *Chiasmocleis* (calls available from 5 of 11 nominal species) and *Elachistocleis* (number of species uncertain). Recordings and audiospectrograms for 3 Asiatic microhylid genera (*Glyphoglossus*, *Kaloula*, and *Microhyla*) are well described by Heyer (1971) and analyses of record-

ings of *Ramanella* are given below. Verbal descriptions are available for four additional Asiatic genera. Of the 10 Asiatic microhylid genera, some call data are now available for all but *Gastrophrynoides* and *Phrynella*. The only Asiatic genera for which call data are available for even half of the species are *Chaperina* and *Glyphoglossus* (both monotypic), *Uperodon* (one of two species) and *Metaphrynella* (both species).

Originals or copies of the recordings analyzed below (Heyer's 1971 analyses and most of the tapes for *Gastrophryne* and *Hypopachus* excluded) are deposited in the American Museum of Natural History, in the University of Texas Bioacoustical Library, and the University of Kansas Museum of Zoology. All recordings were analyzed with an audiospectrograph ("Sona-Graph," Kay Electric Co.). Three graphical displays were utilized: a graph of time (2.4 s) versus frequency (0–8000 Hertz) with frequency resolution by a filter having a 45 Hz band width (narrow band graph), a similar graph utilizing a 300 Hz band width filter (broad band graph), and a graph of frequency (0–8000 Hz) versus intensity (35 decibel range) taken over an interval of 0.05 s (section). Call length, pulse length, and pulse rate were determined from narrow band graphs, except that call lengths longer than about 2.2 s were determined with a stop watch. The dominant frequency was determined either from a section or as the darkest frequency in a narrow band graph (made at an amplification such that one band was distinctly darker than all others). Harmonic intervals (Watkins, 1967; sometimes called fundamentals) were measured as the mean distance between emphasized bands occurring at uniform frequency intervals on either sections or narrow band graphs. Some types of calls do not have a harmonic interval.

DESCRIPTIONS

The available New World microhylid calls can be separated into three discrete groups: bleats, single whistles, and trilled

TABLE 1.—Characteristics of unpulsed mating calls of New World Microhylinae. Figures given are range (top line) and mean \pm standard deviation (lower line) or range of means (marked with *).

Species	Sample	Length (s)	Dominant (Hz)	Harmonic interval (Hz)
<i>Dermatonotus mülleri</i>	2 calls	3.1, 3.9	1500–2200	140–150
		–	1854 \pm 216	146 \pm 5
<i>Hypopachus barberi</i>	11 choruses	0.8–8.2	1750–2900	110–180
		2.4–6.1*	1900–2715*	120–165*
<i>Hypopachus variolosus</i>	26 choruses	0.8–6.0	1500–3600	100–220
		1.0–4.5*	1900–2970*	121–208*
<i>Gastrophryne carolinensis</i>	>9 choruses	0.4–2.4	2400–3900	160–250
		1.0–1.8*	2920–3435*	181–223*
<i>Gastrophryne olivacea</i>	>7 choruses	0.9–3.7	2600–5000	155–280
		1.5–2.5*	3254–4420*	158–238*
<i>Gastrophryne elegans</i>	2 calls	4.0, 5.0	2900–3300	200
<i>Gastrophryne usta</i>	12 choruses	0.5–8.2	3400–4750	70–130
		0.8–5.3*	3510–4350*	90–116*
<i>Elachistocleis</i> sp.	8 choruses (Table 2)	2.0–4.6	2100–4800	125–260
		2.2–4.3*	3097–4429*	140–240*
<i>Glossostoma aterrimum</i>	2 calls	.18, .40	1500–2300	200, 240
<i>Hamptophryne boliviana</i>	16 calls	.35–.46	1100–1500	200–220
		4.1 \pm .04	1234 \pm 120	203 \pm 6
<i>Synapturanus microps</i>	14 calls	.13–.16	1250–1375	= Dominant
		.14 \pm .01	1366 \pm 33	
<i>Arcovomer passarellii</i>	4 calls	.24–.35	3100–3500	"
		.30 \pm .04	3266 \pm 163	
" "	11 calls	.07–.51	2350–5100	"
		.25 \pm .15	3086 \pm 927	

calls. The calls of *Dermatonotus*, *Hypopachus*, *Gastrophryne*, and *Elachistocleis* are similar and consist of a single prolonged note (usually one to several seconds) with a harmonic interval of 100–250 Hz which fluctuates only slightly within any given call. A number of harmonics are present at relative amplitudes within the dynamic range of the graphing technique. The dominant is poorly defined and fluctuates irregularly among two or three adjacent harmonics and, in some cases, passes to a second (non-adjacent) group of two or three harmonics. Verbal descriptions of the calls of this group of genera usually cite the calls as resembling the bleat of a sheep or goat or the sound of an electric buzzer. Mr. Jaime Villa (pers. comm.) encountered a chorus of *H. variolosus* in which frogs and

cattle were apparently answering each others' bleats. The calls of *Glossostoma aterrimum* and *Hamptophryne boliviana* resemble these except in length.

Dermatonotus mülleri (Table 1; Fig. 2A).—Two calls were recorded at Pedro Leopoldo, Minas Gerais, Brazil by W. C. A. Bokermann on 11 February 1965 at 19 C (air) and 23.5 C (water). The species calls while floating in the water (L. D. Vizotto, pers. comm.). The dominant is restricted to two adjacent harmonics. Cei (1956) described the call as a prolonged "báaahh."

Hypopachus barberi (Table 1).—Recordings from 11 localities in Guatemala and Chiapas at water temperatures from 16.5–22 C are discussed by Nelson (1973). Variation in calls within a single chorus is large enough to obscure largely differences because of temperature, mean body size, and geographic location. The dominant occasionally shifts to 700–900 Hz. This species calls while floating in the water, usually with its front feet resting on some support (pers. observ.).

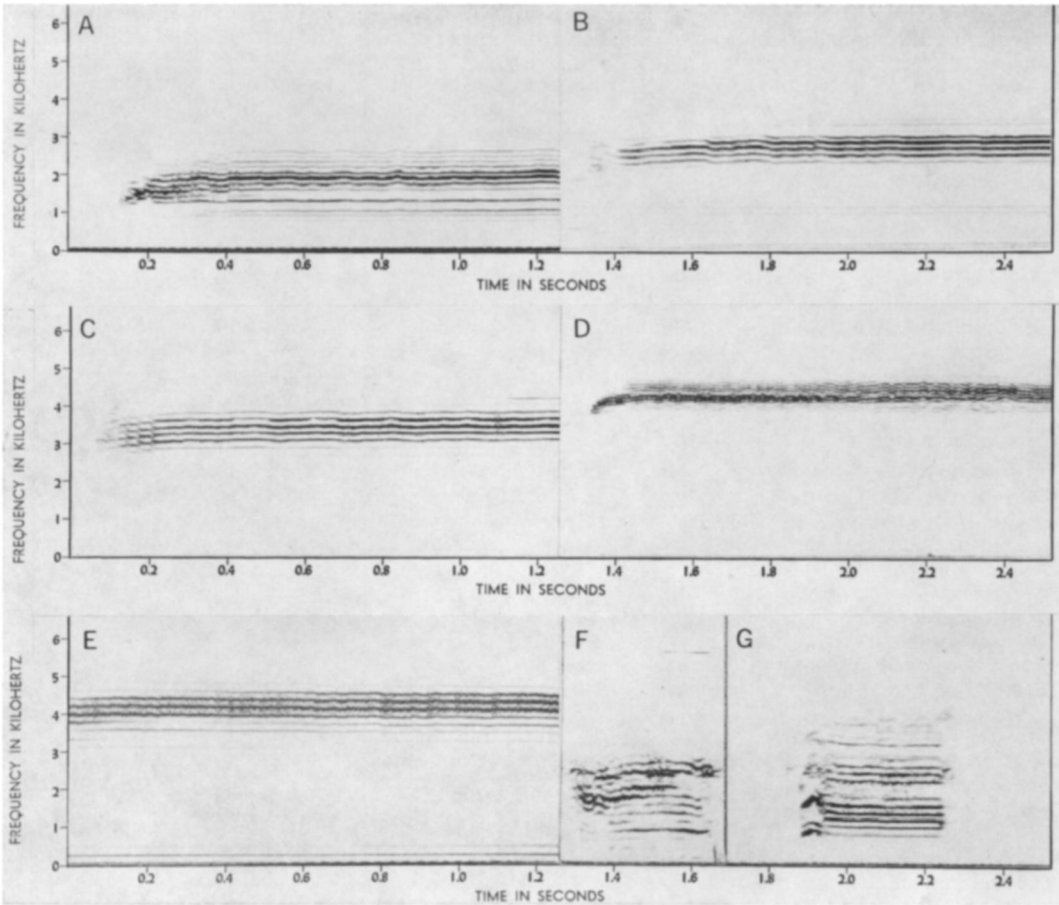


FIG. 2.—Audiospectrogram of mating calls of some New World Microhylinae (I). Background on all audiospectrograms has been suppressed by graphing only the time and frequency range encompassing the desired call. (A) Initial portion of *Dermatonotus mülleri* call from Pedro Leopoldo, Minas Gerais, Brazil at 19 C (air) and 23.5 C (water); (B) initial portion of *Hypopachus variolosus* call from 43.5 km E Amayuca (Morelos) in Puebla, México at 19 C (air) and 23.5 C (water); (C) initial portion of *Gastrophryne olivacea* call from 1.9 km S Mankato, Jewell County, Kansas at 24 C (air) and 22 C (water); (D) initial portion of *Gastrophryne usta* call from 3 km E Escuintla, Escuinta, Guatemala at 29 C (air) and 26 C (water); (E) part of an *Elachistocleis* sp. call from 406 David Simonstratt, Paramaribo, Suriname, at 25 C (air); (F) entire *Glossostoma aterrimum* call from Laguna, Darien, Panamá at 24 C (water); (G) entire *Hamptophryne boliviana* call from Iparia, Peru at 24 C (air?).

Hypopachus variolosus (Table 1; Fig. 2B).—Recordings from 26 localities in Texas, Mexico, and Central America at water temperatures from 18–30 C were studied (CEN, unpubl.). Individual variation obscures any differences produced by body size. The harmonic interval increases at about 5 Hz/°C. At low temperatures the fundamental occasionally shifts to 600–1200 Hz. No geographic differentiation in call was observed.

The behavior of chorusing males varies with numbers and density. At low densities (or in marginal breeding conditions, low temperatures for

example) males usually call from under overhanging or dense vegetation or other protection; at moderate densities males usually call in groups of 6–20 from more exposed positions with their forefeet on a grass stem or other support. At high densities, males swim rapidly around the breeding pool calling almost continuously and attempting to clasp any floating objects. In a chorus at Salamá, Baja Verapaz, Guatemala, *Hypopachus variolosus* were momentarily clasping each other, *Bufo luetkeni*, *Smilisca baudini*, and floating mule feces. These changes with density parallel those noted

by Alexander and Moore (1962) for cicadas. In *Hypopachus*, the response apparently depends on both density and number. Widely scattered males usually call from concealment even though the total number may be large; four or five males in a small pool will be stationary although their local density is high (pers. observ.).

Gastrophryne carolinensis (Table 1).—Nelson (1972a) discussed calls from southeastern United States and compared these with earlier analyses by Blair (1955) and Awbrey (1965). Data are for choruses from 20–32 C (water). No geographic or temperature-related trends are evident in the calls of this species. The data do not permit an analysis of the effect of body size. Calling males float in the water with their forefeet supported on a stem or other objects and with their back strongly arched so that the head is vertical (photo in Wright, 1932).

G. olivacea (Table 1; Fig. 2C).—Nelson (1972a) discussed calls from Kansas, western Texas, Arizona, and Mexico and compared these with earlier analyses by Blair (1955) and Awbrey (1965). Data are for choruses from 19–32 C (water). Unlike other *Gastrophryne*, the call of this species usually begins with a distinct whistle. No direct data are available on variation in call within a single population with changes in temperature or body size. There is appreciable geographic variation which would be comprehensible if the harmonic interval increased from 15–20 Hz/°C and the dominant decreased about 500 Hz/mm snout-vent length (Nelson, 1972a). Calling position is like that of *G. carolinensis* or (at higher chorus intensities) free floating.

G. elegans (Table 1).—Two calls were recorded 13.2 km S Sebol, Alta Verapaz, Guatemala at 25 C (air) by C. E. and S. L. Nelson on 8 July 1964. The calling position is like that of *G. carolinensis*.

G. pictiventris.—This species has not been recorded but N. Scott (pers. comm.) reported that it has a bleat and was calling while floating at the edge of a pool in primary forest at 2 km S Puerto Viejo, Heredia, Costa Rica.

G. usta (Table 1; Fig. 2D).—Recordings from Mexico, Guatemala, and El Salvador at 22–28 C (air) were discussed by Nelson (1972a). The harmonic interval in *G. usta* increases about 6 Hz/°C air temperature; the dominant increases about 150 Hz/°C. The dominant occasionally shifts to 2300–2550 Hz. Unlike other *Gastrophryne*, this species does not call from within the water but rather sits on land, usually under leaves or other cover, within a few meters of the waters edge.

Elachistocleis (Table 2; Fig. 2E).—Call characteristics from the available recordings for this genus are summarized in Table 2. These were variously recorded by W. C. A. Bokermann and field parties from the American Museum, Arizona State University, the University of Kansas, and Indiana University. Considerable confusion exists regarding the number of species of *Elachistocleis* (compare

Carvalho, 1954; Rivero, 1961; Kenny, 1969; Cochran and Goin, 1970; and Nelson, 1972a). For the purposes of the present paper, the consistent form of the call in the various populations allows useful comparisons with other genera. However, the calls (Table 2) are sufficiently heterogeneous, especially in harmonic interval, to suggest that more than one species may be involved.

Elachistocleis typically call from a position similar to that of *G. carolinensis* (pers. observ.; Panama, Venezuela, and Trinidad). Kenny (1969) reported for Trinidad that the call of *E. surinamensis* is “a sustained buzz . . . always given while in the water” and that of *E. ovalis* is “a very high pitched buzzing whistle sustained for up to about 10 to 15 seconds.” Stebbins and Hendrickson (1959) noted that in Colombia *E. ovalis* calls are 1.8–2.0 s long (at 26–28 C water temperature) and similar in sound to those of *Bufo granulosus*. However, Gans (1960) described the calls of *E. ovalis* from Pailon, Bolivia as “a very thin piping whistle” and reported that males call vertically on vegetation with only their hind feet in the water (in contrast to Kenny’s (1969) and my observations). At least some of Gans’ specimens are *Elachistocleis* resembling *E. ovalis*. No easy explanation for Gans’ observation is apparent.

Glossostoma aterrimum (Table 1; Fig. 2F).—The calls attributed to this species on circumstantial evidence were recorded 5 July 1963 by W. E. Duellman and students at Laguna, Darien, Panama at 24 C (water). *G. aterrimum* were sitting in the water when captured but were not actually observed to emit these calls. Unfortunately, the tape speed during the recording was erratic; of five calls on the tape two seem to have been undistorted and the other three plausibly could be derived from these two by fluctuating tape speed. If this interpretation is correct, *G. aterrimum* has a call resembling a very brief segment of a *Hypopachus* or *Elachistocleis* call.

Glossostoma aequatoriale.—Male release calls from 12 km E Cuenca, Azuay, Ecuador were recorded 17 November 1968 by C. E. and S. L. Nelson at 12.5 C (air) and 17 C (water). The release calls are untrilled, short (.05–.06 s), and have a dominant frequency at 1500–2800 Hz ($\bar{x} = 2252 \pm 411$) for 17 calls.

Hamptophryne boliviana (Table 1; Fig. 2G).—This species was recorded 15 January 1963 at Iparia, Peru at 24 C (air?) by J. P. Bogert who reported (pers. comm.) that the species calls while floating, much like *Hypopachus*. The calls resemble those of *G. aterrimum*, but two distinct sets of emphasized frequencies are present. Calls of *H. boliviana* and *G. aterrimum* subjectively are short “beeps” and not a bleat like those of the preceding genera.

Three monotypic New World genera have very simple whistles: *Synapturanus*, *Myersiella*, and *Arcovomer*.

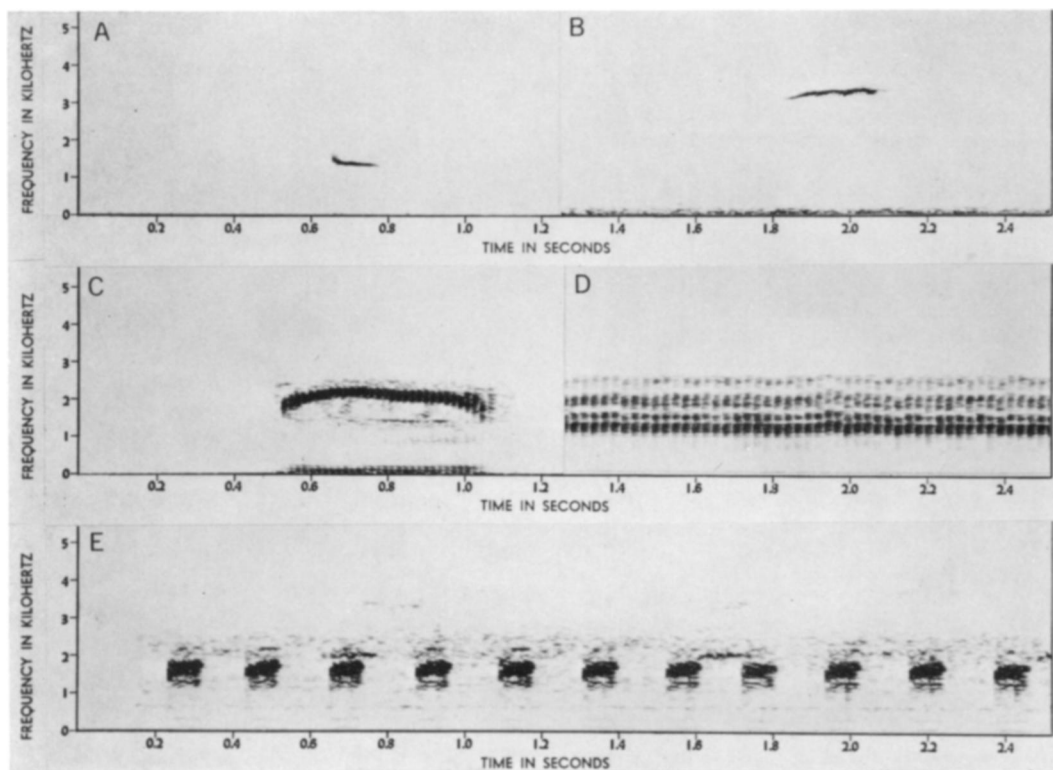


FIG. 3.—Audiospectrograms of mating calls of some New World Microhylinae (II). (A) Entire *Synapturanus microps* call from Sipaliwini Airstrip, Suriname, no temperatures given; (B) entire *Arcovomer passarellii* call from Itaguai, Rio de Janeiro, Brazil at 24 C (air); (C) entire *Dasytops schirchi* call from Sooretama, Linhares, Espírito Santo, Brazil at 20 C (air); (D) part of a *Ctenophryne geayi* call from the junction of the Rios Ariari and Guavaire, Vaupes, Colombia at 27.7 C (air); (E) part of a *Stereocyclops incrassatus* call from Sooretama, Linhares, Espírito Santo, Brazil at 20 C (air).

Synapturanus microps (Table 1, Fig. 3A).—This species was recorded at Sipaliwini Airstrip, Suriname on 10 February 1970, by M. S. Hoogmoed who reports (pers. comm.) that the species was “calling in large numbers from subterranean sites during rain at the edge of the forest” at a depth of 4–5 cm at midnight. This call is a single, brief, nearly pure tone (a harmonic at twice the dominant is present but several decibels fainter than the dominant).

Myersiella subnigra.—This species has not been recorded but Izecksohn et al. (1971) reported that “the voice, when at low intensity somewhat resembles those of the whistling *Leptodactylus*; when loud it suggests the note of the cuculid *Crotophaga ani*.” *C. ani* notes are about 0.3 s long and rise in dominant from 1000 to 2200 Hz (Robbins et al., 1966). Izecksohn et al. (1971) also report that *M. subnigra* calls on the forest floor from under the adventitious roots of shrub-like Piperaceae, nests in cavities below the leaf layer on the ground, and has direct development.

Arcovomer passarelli (Table 1, Fig. 3B).—This species was recorded by W. C. A. Bokermann at Itaguai, Rio de Janeiro, Brazil at 24 C (air?) on 23 January 1965 (4 calls) and by E. Izecksohn and C. E. and S. L. Nelson at Horto Florestal de Santa Cruz, Itaguai, Rio de Janeiro (state), Brazil, at 22 C (air) on 9 December 1968 (11 calls). This species calls while sitting beside land crab burrows in which it seeks refuge if disturbed. The call is a short clear tone having a single weak harmonic.

The remaining New World microhylinae calls have the common feature that they are distinctly trilled or slowly pulsed.

Dasytops schirchi (Table 2; Fig. 3C).—This species was recorded at Sooretama, Linhares, Espírito Santo, Brazil at 20 C (air) by W. C. A. Bokermann, on 10 November 1964. The dominant rises approximately 400 Hz in the first 0.1 s of the 0.5–0.6 s call and falls a similar amount in the last 0.2–0.3 s. Although the dominant band is broad (about 300 Hz) no harmonic structure is evident.

TABLE 2.—Characteristics of the mating calls of *Elachistocleis* from various localities. Figures for call parameters are range (top line) and mean \pm standard deviation (second line).

Locality	Air °C		Calls	Length (s)	Dominant (Hz)	Harmonic interval (Hz)
		water °C				
Brazil, São Paulo, Campo Grande, Santo Andre	14/—		4	3.2–4.1 3.7 \pm 0.5	2100–3600 3097 \pm 414	180 —
Colombia, Meta, ca. 15 km N Villavicencio	20.7/24		6	3.0–4.6 4.3 \pm 0.6	3500–4200 3820 \pm 227	160–200 189 \pm 18
Venezuela, Bolivar, near Villa Lola	24/24		37	2.0–4.1 2.9 \pm 0.5	3650–4150 3834 \pm 157	125–142 140 \pm 7
Panamá, Chiriquí, David	—/24		5	2.2–4.2 2.9 \pm .05	3400–3600 3500 \pm 100	200 —
Suriname, Paramaribo	25/—		9	2.1–2.4 2.3 \pm 0.1	4000–4200 4133 \pm 71	200–220 211 \pm 7
Trinidad, 1.6 km SE Tunacuna	25/—		15	1.3–1.7 1.6 \pm 0.2	4100–4300 4133 \pm 59	100–112 102 \pm 4
Panamá, Panamá, Cerro la Compañía	—/25.2		4	2.0–4.0 2.9 \pm 1.0	3000–4100 3450 \pm 384	167–220 210 \pm 42
Panamá, Panamá, 4.8 km S Bejuco	—/25.5		8	2.0–3.0 2.2 \pm 0.4	2400–4150 3860 \pm 173	220–260 240 \pm 9
Guyana, Rupununi, Lethem, Manari Ranch	26.7/25.5		8	2.3–2.6 2.5 \pm 0.1	4000–4800 4425 \pm 242	244–260 255 \pm 7
Panamá, Chiriquí, 52 km E David	—/26		13	1.4–4.6 2.7 \pm 1.6	3000–4000 3455 \pm 230	200–230 208 \pm 11
Venezuela, Monogas, 15 km S Maturín	26/26		2	2.1, 2.4 —	4000, 4200 —	216, 220 —
Venezuela, Apure, San Fernando de Apure	27.8/26.7		1	2.3 —	4700 —	113 —

Ctenophryne geayi (Table 2; Fig. 3D).—This species was recorded by W. F. Pyburn at the junction of the Rios Cafre and Guaviare (about 20 km W San Jose del Guaviare), Vaupes, Colombia at 27.7 C (air) on 28 June 1969. The call is a prolonged trill. The males were calling on dry land from under leaf litter at edge of slough (W. F. Pyburn, pers. comm.).

Chiasmocleis bicegoi (Table 2; Fig. 4A).—Calls of this species collected 11–12 December 1968 at Horto Florestal de Santa Cruz, Itaguai, Rio de Janeiro, Brazil were recorded 15 December 1968 at 24–25 C while kept in a styrofoam cooler by C. E. and S. L. Nelson.

Chiasmocleis leucosticta (Table 2; Fig. 4B).—This species was recorded by C. E. and S. L. Nelson at 10 km W Casa Grande, Sao Paulo, Brazil at 18 C (air and water) on 1 December 1968. The males were calling with their bodies extended semivertically, head up, along vegetation or steep areas of the bank and with their hindquarters in or near the water.

Chiasmocleis panamensis (Table 1; Fig. 4C).—Calls from 4 choruses in the Canal Zone of Panama are discussed by Nelson (1972b). The call is a short, trilled whistle. The dominant is apparently

independent of temperature over a range of water temperatures of 23–27.7 C, but the trill rate increases at about one note/s/°C and the mean number of notes per call decreases about 1.7 notes/°C over the same range. The males call with the body extended vertically along a weed stem, head up, with about one-third of the body in the water.

Chiasmocleis schubarti (Table 2; Fig. 4D).—This species was recorded at Sooretama, Linhares, Espírito Santo, Brazil at 19.5 C (air?) by W. C. A. Bokermann on 9 November 1964. The call is a prolonged insect-like chirping.

Chiasmocleis ventrimaculata (Table 2).—Recordings of this species are in the background of a recording made by W. F. Pyburn at the junctions of the Rios Cafre and Guaviare, Vaupes, Colombia, at 27.7 C (air) on 28 June 1969. As the call is scarcely detectable, the values given are approximate. Males were calling from under leaf litter at the edge of a slough (W. F. Pyburn, pers. comm.).

Stereocyclops incrassatatus (Table 2; Fig. 3E).—This species was recorded at Sooretama, Linhares, Espírito Santo, Brazil by W. C. A. Bokermann at 20 C (air) on 10 November 1964. This species calls while floating in the water (E. Izecksohn, pers. comm.). The call resembles those of

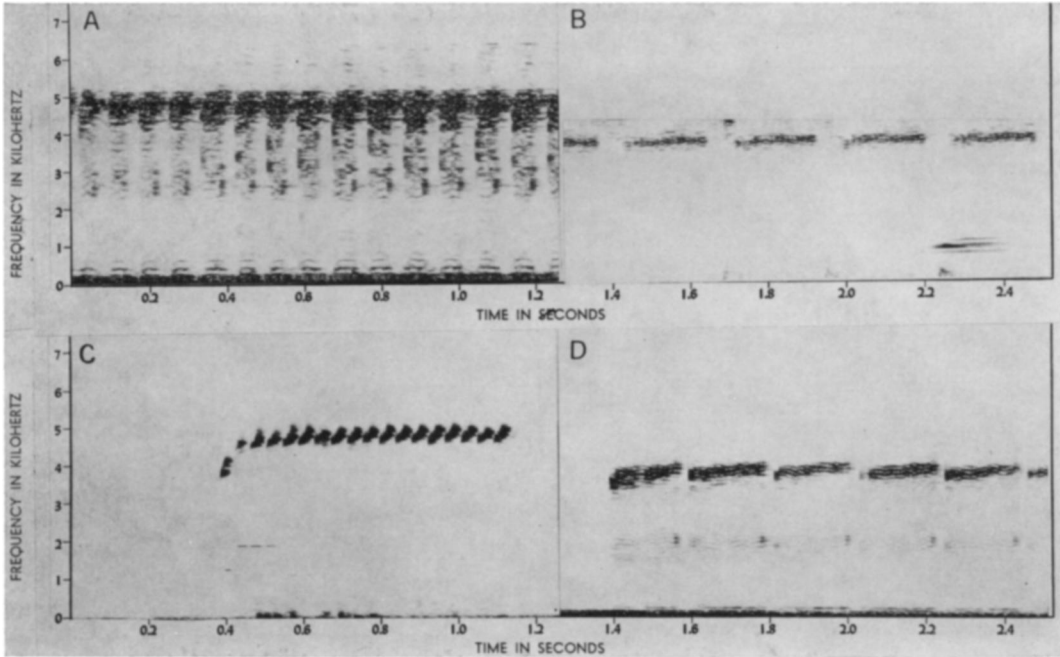


FIG. 4.—Audiospectrograms of mating calls of *Chiasmocleis*. (A) Part of a *C. bicegoi* call from Horto Florestal de Santa Cruz, Itaguaí, Rio de Janeiro, Brazil at 24–25 C (air); (B) part of a *C. leucosticta* call from 10 km W Casa Grande, São Paulo, Brazil at 18 C (air and water); (C) entire *C. panamensis* call from Panamá Canal Zone, Panamá at 20 C (air) and 25 C (water); (D) part of a *C. schubarti* call from Sooretama, Linhares, Espírito Santo, Brazil at 19.5 C (air?).

Chiasmocleis leucosticta, *C. schubarti* and *C. ventrimaculata* except that the notes are shorter and the time between them longer. The pulse rates are similar (Table 2) but the call seems more distinctly pulsed to the human ear.

As the calls of the Asian Microhylinae cannot be easily separated into groups, they are presented in the sequence used by Parker (1934).

Glyphoglossus molossus (Table 4).—Calls were described and figured by Heyer (1971). In addition to the features he described the audiospectrogram also shows a harmonic interval of about 200 Hz and an increase of pitch of each harmonic throughout the call of about 300 Hz with shifts in emphasized harmonics maintaining an approximately constant dominant frequency.

Uperodon globulosum.—Calls resemble “the bleating of a goat” (Kirtisinghe, 1957).

Kaloula pulchra (Table 4).—Calls from Thailand were described and figured by Heyer (1971). Additional series (Table 4) from 2 choruses near Warakapola, Western Province, Ceylon, both recorded by C. M. Bogert on 28 April 1956 are significantly different from each other and from the Thailand series. Means (\pm SD) from 10 calls in each of the Ceylon series are for length (a) 0.6 ± 0.1 and (b) 0.45 ± 0.1 s, for dominant (a)

490 ± 32 and (b) 611 ± 93 Hz and for pulse rate (a) 61 ± 4 and (b) 66 ± 3 /s. Parker (1934) erected *K. pulchra taprobanica* for Ceylonese specimens of this complex. The differences in dominant and pulse rate between Ceylon and Thailand thus parallels morphological differences and suggests the Ceylonese populations may be a distinct species. Bourret (1942) described the calls of *K. pulchra* as a lowing or roaring sound.

K. borealis.—This species calls: “wreck-wreck” and “urrh-urrh” (Shannon, 1956).

K. conjuncta.—Calls are “chuck-chuck-chuck” (Alcala, 1962).

K. macrotypica.—The males “croak with a deep sound very much like that of *rugifera* and *borealis*” (Liu, 1950).

K. picta.—Calls are “ack-ack” (Inger, 1954).

K. rugifera.—This species croaks with a deep sound much like that of *Kaloula borealis*; calling males float in the water sometimes with the forefeet supported on vegetation (Liu, 1950).

Ramanella obscura (Table 4).—Two calls were recorded at Horton Plains, Ceylon (2260 m) by C. M. Bogert on 26 April 1965 at 18 C (air).

Ramanella variegata.—Calls approximate “qhauy-qhauy” (Kirtisinghe, 1957).

TABLE 3.—Characteristics of pulsed mating calls of New World Microhylinae. Figures for call parameters are range (top line) and mean \pm standard deviation (second line). See text for localities.

Species	Sample	Length (s)	Dominant (Hz)	Pulse rate (s^{-1})	Pulse length (s)	Pulses call	Harmonic interval (Hz)
<i>Dasylops schirchi</i>	10 calls	.54-.60	800-2500	52-58	.02 ²	30-32	-
		.58 \pm .02	1942 \pm 544	55 \pm 2	-	31 \pm 1	-
<i>Ctenophryne geayi</i>	5 calls	4.6-4.7	1100-1300	37-39	.03 ²	172-183 ²	-
		4.7 \pm 0.1	1190 \pm 88	39 \pm 1	-	-	-
<i>Chiasmocleis bicegoi</i>	5 calls	1.8-5.0	4465-4650	11-13	.05-.07	19-65 ²	-
		3.4 \pm 1.4	4529 \pm 71	11.8 \pm 1	.06 \pm .01	-	-
<i>Chiasmocleis leucosticta</i>	6 calls	7.5-16.8	3400-4000	3.3-4.4	.15-.25	25-66	72-75
		12.4 \pm 4.2	3647 \pm 177	3.8 \pm 1	.21 \pm .03	46 \pm 17	73 \pm 1
<i>Chiasmocleis panamensis</i>	4 choruses	.44-.61	4800-5500	25-30	.03-.04 ²	11-18	-
		.49-.72 ¹	5122-5280 ¹	26-30 ¹	-	13.8-15.5 ¹	-
<i>Chiasmocleis schubarti</i>	2 calls	5.1, 6.0	3700-4100	4.6	.20-.24	22, 27	105
		-	3886 \pm 136	-	.22 \pm .01	-	-
<i>Chiasmocleis ventrimaculata</i>	1 segment	-	3350-3700	-	.10-.18	-	-
		-	3562 \pm 110	-	.13 \pm .01	-	-
<i>Stereocyclops incrassatus</i>	1 segment	>7	1500-2000	4.7	0.8	-	100
		-	1740 \pm 88	-	-	-	-

¹ Range of means given in place of mean \pm standard error when multiple localities are summarized.

² Pulse length estimated as (pulse rate)⁻¹; pulse per call estimated as (pulse rate) \times (duration).

Kalophrynus pleurostima.—Calls sound like an insect (Bourret, 1942). The males call from water-holes at the base of trees and sometimes lay eggs in holes in logs (Inger, 1956).

Chaperina fusca.—The call is a "relatively low pitched buzz"; they call in groups of 10 or more (R. F. Inger, pers. comm.).

Metaphrynella pollicaris.—Calls resemble a note of a flute (Bourret, 1942).

M. sundana.—Calls are "piping low-pitched whoots" or short (about one-third s) pure whistles with a moderately high pitch that rises at the end of the whistle; the males call from tree holes containing water (Inger, 1956, and pers. comm.).

TABLE 4.—Characteristics of mating calls of Asiatic Microhylinae. Figures given are ranges. Asterisk indicates data taken from Heyer (1971).

Species	Length (s)	Dominant (Hz)	Pulse rate (s^{-1})	Comments
<i>Glyphoglossus molossus</i> *	0.30-1.32	300-1100	40-59	Harmonic interval 300 Hz, partially pulsed
<i>Kaloula pulchra</i>				
Thailand*	0.56-0.60	250	27-30	Partially pulsed
Ceylon (a)	0.5-0.8	400-500	54-68	-
Ceylon (b)	0.4-0.5	500-700	60-70	-
<i>Ramanella obscura</i>	0.4	2200	-	Harmonic interval
<i>Microhyla achatina</i>	0.5-0.9	3000-3200	14-20	91-100 Hz
<i>M. berdmorei</i> *	0.09-0.26	1500-1800	33-35	-
<i>M. butleri</i> *	0.16-0.21	1200-4500	28-44	Data given for each note, 3-5 notes per call
<i>M. heymonsi</i> *	0.48	1700-3000	23	Harmonic interval 160 Hz, partially pulsed
<i>M. inornata</i> *	0.79-2.02	4400-6500	66	-
<i>M. ornata</i> *	0.23-0.31	1200-3500	53-60	-
<i>M. pulchra</i> *	1.4-1.9	2000-2500	7-10	-
				-

Microhyla achatina (Table 4).—Calls were recorded by R. G. Zweifel at Tjibodes, Java (1400 m) on 11 June 1968 at 18.2 C (air) and at 17.8 C (also air). The mean (\pm SD) values of the call parameters are: length 0.7 ± 0.1 s, dominant 3105 ± 80 Hz, and pulse rate 16.6 ± 2.2 /s for 19 calls.

M. berdmorei (Table 4).—Calls were described and figured by Heyer (1971).

M. butleri (Table 4).—Calls were described and figured by Heyer (1971); from his figure it is evident that this call has a harmonic interval of about 160 Hz. The call sounds "like the gritting of human teeth" (Taylor, 1962).

M. heymonsi (Table 4).—A call was described and figured by Heyer (1971). The call is a repeated "cricket-like note" (Pope, 1931) or a series of "sharp clicks" (Bourret, 1942).

M. inornata (Table 4).—Calls were described and figured by Heyer (1971).

M. ornata (Table 4).—Calls were described and figured by Heyer (1971). Calling males "may float on the water or support the anterior part of the body on vegetation" (Liu, 1950).

M. pulchra (Table 4).—Calls were described and figured by Heyer (1971). Bourret (1942) noted that the call of *M. pulchra* consists of a single note and contrasts thereby with the two-noted call of *M. ornata*; neither description is easily reconcilable with Heyer's (1971) audio-spectrograms.

DISCUSSION

Phylogenetic Implications.—Mating calls of four New World microhylid genera (*Dermatonotus*, *Elachistocleis*, *Hypopachus*, and *Gastrophryne*) are prolonged, single notes with no systematic change during the call. Of 21 Asiatic microhylines for which some call data are available, 18 (including 7 *Microhyla*) clearly do not have *Hypopachus*-like calls; only the verbal descriptions for *Uperodon globulosum* and *Kalophrynus pleurostigmata* cannot be definitely excluded (but neither can these be said to have this call type without further data). Call data thus support Carvalho's (1954) suggestions that *Gastrophryne* is closely allied to *Hypopachus* and not closely allied with Asiatic *Microhyla* and that *Elachistocleis* and *Hypopachus* are allied to *Dermatonotus*.

The calls of *Glossostoma aterritum* and *Hamptophryne boliviana* are similar to those of *Dermatonotus*, except in length. Carvalho (1954; my Fig. 1) suggested that *Glossostoma* is close to *Dermatonotus*, but

placed *Hamptophryne* in another grouping. The similarities of the call of *Hamptophryne* to that of *Glossostoma* either must be regarded as convergent or the affinities of the genus must be re-evaluated. Of the Asiatic calls studied only those of *Ramanella obscura* and the individual notes of that of *Microhyla butleri* resemble those of *Hamptophryne*. The call of *Glyphoglossus molossus* superficially resembles that of *Hamptophryne* but differs in internal structure (upward drift of each harmonic, replacement of emphasized harmonics). These resemblances are presumably convergent.

Synapturanus microps and *Arcovomer passarelli* calls are single, short, pure notes. Verbal descriptions of the calls of *Myersiella subnigra*, *Metaphrynella pollicaris* and *Metaphrynella sundana* suggest similar calls. In each of these species the males call individually from burrows or tree holes apparently within their normal activity ranges rather than congregating at bodies of water. A number of non-microhylid frogs which also call from uncongregated sites also use short, relatively pure notes (*Cochranella*, *Eleutherodactylus* and *Syrhophus* are examples). As is discussed below, the characteristics of these calls are those expected to minimize locatability by predators. Consequently the similarities between these calls could reasonably represent convergence. However, Carvalho (1954) stated that *Synapturanus* and *Myersiella* are closely allied, a suggestion that is supported by the unusually large ovarian eggs in both species (Izecksohn et al., 1971); thus for this pair the similarity in call appears to be homology.

The calls of *Dasypops schirchi*, *Ctenophryne geayi*, *Microhyla heymonsi*, *M. butleri*, and *M. ornata* are all relatively untuned, rapid trills with very short notes (.02-.04 s). *Stereocyclops incrassatus*, *Chiasmocleis bigeoi*, *C. leucostica*, *C. schuberti*, and *C. ventrimaculata* have similar trills but the notes are longer (.05-.25 s). *M. berdmorei* has a similar call with only a few notes. *Chiasmocleis panamensis* has a higher pitched trill with shorter notes which is clearly different from those of other *Chia-*

smocleis. *Microhyla inornata* has a high-pitched trill with a trill rate (66/s) that approaches the time resolution limit of the narrow band graph. The presence of trilled calls in *Stereocyclops*, *Ctenophryne* and *Chiasmocleis* matches Carvalho's (1954) suggestions of affinity (Fig. 1). The call of *Dasylops* seems more similar to this group than to the *Dermatonotus* group with which Carvalho (1954) suggested affinity. Note, however, that a doubling of the pulse rate would transform a *Dasylops* call into a short bleat not unlike that of *Glossostoma*. The resemblance of the *Microhyla* calls to those of *Dasylops*, *Stereocyclops*, *Ctenophryne*, and some *Chiasmocleis* may either represent convergence or the retention of a primitive type of call; Heyer (1971) suggested that the Asiatic calls could be derived from a pulsed prototype having energy over a broad range of frequency.

The coloration and web of *Chiasmocleis schubarti* clearly ally it with the members of Dunn's (1949) *C. leucosticta* species group (including *C. ventrimaculata*) from which both *C. panamensis* and *C. bicegoi* are distinct. The similarities of the calls of *C. leucosticta*, *C. ventrimaculata* and *C. schubarti* and the relative distinctness of those of *C. bicegoi* and *C. panamensis* thus match Dunn's (1949) suggestions of affinity.

The call of *Kaloula pulchra* shows no clear affinity with those described for any other microhylinae genus. The verbal descriptions for other species in this genus (Alcala, 1962; Inger, 1954; Kirtisinghe, 1957; and Shannon, 1956) are compatible either with similarity to *Kaloula pulchra* or with trilled calls depending on the prolongation and repetition rate envisioned for the syllables representing the call.

I know of no other cases in which anuran mating calls have been shown to have similarities suggestive of intergeneric affinities. Marler (1957) suggested that mating calls should rapidly diverge because species-specificity is fundamental to their function, a suggestion with which most subsequent workers have concurred; however, Lanyon (1969) cites several cases

where suprageneric affinities in birds appear to be reflected in their calls. The intergeneric similarities evident from the calls of New World microhylines could be interpreted either as representing a case where calls have been conservative, perhaps because the number of sympatric species is low, or a case where taxonomic distinctions have been unusually fine, as suggested by Blair (1962).

Ecological Considerations.—Marler (1955, 1957) and Marler and Hamilton (1966) considered the physical properties of sounds which affect the ease with which they are located by the binaural system of vertebrates. Perceptible differences between the ears in intensity, phase, or time of arrival increase the ease with which a sound can be located. Intensity difference detection depends on sound shading by the head and becomes efficient only for frequencies having wavelengths less than the width of the head (wavelength is proportional to frequency; the wavelength for 7 kHz is about 5 cm). The use of very high frequencies is restricted by greater attenuation with distance (energy attenuation over a given distance is inversely proportional to the square of the frequency; Konishi, 1970) and by reflection off objects larger than its wavelength. Marler (1955) suggested that the refractory period of nerves probably limits the use of phase differences to frequencies below 1 or 2 kHz and that phase differences are ambiguous for frequencies having wavelengths more than twice the distance between the ears. Time differences can be used at any frequency and are most efficiently detected for sounds having abrupt discontinuities, such as pulses, or transient frequencies (phase difference location requires a relatively sustained sound). Sound location is easiest for sounds which have wide frequency range and provide both low frequencies for phase differences and high frequencies for intensity differences and are pulsed or have transients for time differences, "a series of clicks or pips provides the maximum number of clues" (Marler and Hamilton, 1966). Sounds can be made difficult to locate "by eliminating time cues,

so that the sound fades in and out with no abrupt discontinuities. A pure tone is used pitched above the frequency maximum for phase difference location but below the optimum for generating binaural intensity differences. Such a sound, a high thin whistle has a ventriloquial quality . . ." (Marler and Hamilton, 1966). Hawk-alarm calls, nestling and some fledgling calls fit this model as do alarm calls of many mammals, many orthopteran songs, and the alarm calls of Amphibia (Marler, 1957). Marler (1955) also suggested that chorusing is an alternative way of making a particular individual difficult to locate. In considering the applications of these ideas to frog calls it is useful to note that the small head size of frogs would, with Marler's constraints, make the use of phase differences impossible and restrict the use of intensity differences to frequencies well above those at which most frog calls have their maximum energy, thereby suggesting that binaural detection of direction of calling males by receptive females is largely based on time differences. Konishi (1970) suggested that communication in areas of dense vegetation ("jungle floor") should use relatively low frequencies whereas communication in open spaces should use higher frequencies and wider frequency ranges.

The dominant frequency of a resonator or vibrator decreases as its size increases; if larger frogs have larger vocal pouches or vocal cords they might be expected to have lower dominant frequencies than smaller species to which they are allied.

Heyer (1971) noted that *Glyphoglossus* and *Kaloula* are large forms that float while calling in large choruses and that they had the lowest dominant frequencies of the Asiatic Microhylidae he studied whereas the other species (*Calluella* and six species of *Microhyla*) had higher dominant frequencies and called "from the banks or from vegetation on the water surface" and are smaller. He suggested that in *Glyphoglossus* and *Kaloula* "the females need only to locate the ponds, not individual males." The inverse correlation of dominant frequency with size generally holds for New

World microhylines: the relative sizes of the descending order are, for forms with pulsed calls, *Stereocyclops*, *Dasylops*, *Ctenophryne* and *Chiasmocleis* and for those with prolonged bleats, *Dermatonotus*, *Hypopachus*, *Elachistocleis*, and *Gastrophryne* and this is the general ordering of the dominant frequencies within each group (*Elachistocleis* is a partial exception). All of the long-bleat group (except *G. usta*) and *Stereocyclops*, and *Hamptophryne* have males which float while calling (typically with their front feet resting on a support), *Ctenophryne* and *Chiasmocleis* call from the edge of the water, and *G. usta* call from within a few meters of the water. In the New World Microhylinae, the influence of size, but not that of chorus position (along shore or floating), is thus evident on the dominant frequencies.

In the American genera *Arcovomer*, *Synapturanus*, and *Myersiella* (probably), and the Asiatic genus *Metaphrynella* males apparently call from dispersed sites on the forest floor and have high pitched calls which are similar to hawk-alarm calls of various passerines and which match the criteria for a hard-to-locate, predator-confounding call. The calls of the New World forms thus do not seem to have a lower pitch on the tropical forest floor nor is there any correlation evident between habitat and pitch (compare Konishi, 1970).

The shift from stationary to actively swimming with increasing chorus size and density in *Hypopachus variolosus* could be adaptive both in competition for mates and in avoiding predators. At low densities the predominant factor determining which males mate may be choice by the female of an individual male's call. A swimming male might stand relatively little chance of encountering a female as she could not home on his call. At moderate densities however, males are often spaced at less than 15 cm from their nearest neighbors and a female approaching any one is likely to disturb some of the others and be clasped by them as described by Awbrey (1965) for *Gastrophryne olivacea*. At higher densities the probability of a cruising male

clasping a female responding to the call of another male should exceed the chance of a female making an approach to a selected male without being clasped by another male. Behavior thus might be expected to shift from stationary to moving. At low densities of hidden males, the yield per unit effort of a collector, and presumably of a generalized predator, is relatively low. At moderate densities many frogs are discovered accidentally. Since moving frogs are more difficult to capture, the chance of individual survival may switch at some density from favoring a stationary male to favoring a moving male.

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REPRODUCTIVE BIOLOGY OF THE ANGUID LIZARD, *GERRHONOTUS COERULEUS PRINCIPIS*

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ABSTRACT: Monthly samples of male and female *Gerrhonotus coeruleus principis* were collected in coastal Washington. Reproductive condition of both sexes was recorded as well as body, air and substrate temperatures. Basking behavior in late fall and early spring coincides with the period of active spermatogenesis. Ovulation and mating occur from late April through mid-June. Young are born from mid-August through mid-September. Testes are in a regressed state during mid-summer. Adult lizards are gregarious during late fall and early spring, being relatively abundant at localized hibernation sites. Lizards are not gregarious during summer. This species has a typical temperate zone lizard reproductive cycle.

THE purpose of this study is to present information dealing with the reproductive cycle of *Gerrhonotus coeruleus principis*. Ecological data not previously reported but pertinent to the reproductive biology are also presented.

Studies on the genus *Gerrhonotus* include natural history (Fitch, 1936), taxonomy (Fitch, 1938; Tihen, 1949; Stebbins, 1958), anatomy (Tihen, 1949; Criley, 1968), and thermal relations (Brattstrom, 1965; Cunningham, 1966; Dawson and Templeton, 1966; Vitt, 1971). Data on reproduction are mostly natural history notes. Greer (1967), Stebbins (1954), and Fitch (1936) have recorded only numbers of eggs or offspring and time of mating or hatching.

G. c. principis is common in cool humid environments of northwestern United States, often in the vicinity of coniferous forests

(Fitch, 1936). It ranges from British Columbia south to northwestern California and east to western Montana (Gordon, 1939; Carl, 1968), and inhabits primarily the transition life zone.

MATERIALS AND METHODS

Work was carried out primarily during 1969 and 1970 although field data from March 1966 through June 1970 are included. In addition, data from several individuals collected in June 1972 are included. Monthly collections were made except in November and December during which time the lizards were inactive. The study area encompassed approximately 5.12 km² extending along Chuckanut Drive, 1.6 km south of Bellingham, Whatcom County, Washington. Lizards were collected by hand in rocky outcroppings from slopes or talus slides.