

Call Differences and Calling Site Segregation in Anuran Species from Central Amazonian Floating Meadows

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Summary. The acoustic behaviour of 15 sympatric and synchronically breeding species of frogs in an area of floating meadows near Manaus (Brazil) was studied for a period of 8 months. The calling positions of each species can be identified with certain physiognomic types of vegetation.

Sound analyses were used to compare the mating calls. The main variables are dominant frequency, call duration and pulse repetition rate. Each of the 15 species has a distinct mating call and differs from the acoustic behaviour of each other one. Eleven species are separated in their dominant frequency ranges within their specific calling sites. Species sharing emphasised frequency ranges within identical calling sites differ greatly in at least two temporal variables.

The roles of calling position, spectral, and temporal features of mating calls in species recognition and premating reproductive isolation are discussed.

Introduction

Tropical anuran fauna exhibits great diversity, unusual to temperate zones. The multiplicity of equatorial forest species has been interpreted as the result of recurrent geographic isolation due to drastic paleoclimatic changes (Schjøtz, 1967; Haffer, 1969; Vanzolini and Williams, 1970). The wide variety of species and the abundance of many closely related sympatric species of tropical Anurans have attracted several investigators to study interspecies interactions (Duellman, 1967; Crump, 1971, 1974).

Studies on sympatric and synchronically breeding anuran species have led to the conclusion that differences in mating calls may serve as an important mechanism in preventing mismatings (Blair, 1956, 1958, 1964; Duellman, 1967; Littlejohn, 1969; and others). Ethologic experiments (Martof and Thompson, 1958; Gerhardt, 1974) and neurophysiologic studies (see Capranica, 1976, for summary) revealed species selectivity in their auditory systems. These results

confirm the biologic significance of the mating call as a primary species-detecting mechanism.

The purpose of this paper is to present analyses and interpretations of mating calls and calling stations of 15 Central Amazonian anuran species, breeding at the edge of or within temporary mats of floating vegetation. The possible isolating effect of calling site segregation and of distinct call structures is discussed.

Methods

Field observations were conducted at least twice a month at the study area near Manaus from November 1974 to January 1975 and from March until the first week of August of the same year. During the first week of July a 20-m wide section of a floating meadow was measured to illustrate the distribution of aquatic plants at high-water level (Fig. 1). Species covering more than 80% of a square meter were designated by a capital letter. Dominant species, representing an estimated portion of 50 to 80%, are listed in capital letters in combination with small letters, representing species amounting to 20% or more. Aquatic plants covering less than a fifth of a square meter were not recorded in these measurements. Notes on the calling stations of all species described in this study were made throughout the observation period at the study site and at other floating meadows found along the lower Solimoes and Purus rivers. Data were gathered on *Leptodactylus wagneri* (Leptodactylidae), *Lysapsus limellus laevis* (Pseudidae), and 13 hylid species. With the exception of *Hyla rossalleni* (14 individuals), *Hyla boans* (24), and *Hyla eglerti* (37), more than 100 calling individuals were observed for each species.

All calls were recorded at 19 cm/s using a UHER 4000 Report L tape recorder and a UHER dynamic microphone. Spectral characteristics of calls were analysed with a Kay 7030 A Vibralyzer (overall response in FL-1). Dominant frequency bands were determined for each individual call from contour displays and measured to the nearest 100 cps. Absolute ranges of these bands are given for each species (see Table 3 and Fig. 6). The average in the arithmetical means of the dominant frequency bands is listed as dominant frequency. In Table 3, additional data are given for calls of *Hyla raniceps* and *Leptodactylus wagneri*, for which a second separated, almost equally dominating spectral band can be found. Measurements of temporal characteristics were obtained from oscillograms made with a Tektronix 564 B storage oscilloscope or a Tektronix 502A oscilloscope and a Toennies Recordine camera at a speed of 250 mm/s. Duellman's (1970) terminology of call structures is used predominantly in the description of the vocalisations.

Description of the Study Area

The study area is situated within the inundation area of the Solimoes (= Middle Amazon) river at the SW end of Lago Janauari (3°13'S and 60°02'W). Climatic data from a meteorologic station at Reserva Ducke (3°08'S and 60°02'W) (INPA, boletim meteorológico, 1974, 1975) and data on the fluctuation of the Rio Negro water level at Manaus are given in Figure 2. The distribution of aquatic plants fluctuates throughout the year. With rising water level the floating vegetation develops explosively and expands until it reaches its full extension during the high-water period. With falling water level the floating meadows degenerate rapidly (Junk, 1970).

The floating vegetation was divided into 3 categories (see Figs. 1 and 3). Aquatic plants distributed flatly over the water surface with hardly any vertical structures form the first category (i.e., 'Salvinia vegetation') of which *Salvinia auriculata* was the dominant species. *Limnobium stoloniferum*, *Ludwigia helmin-*

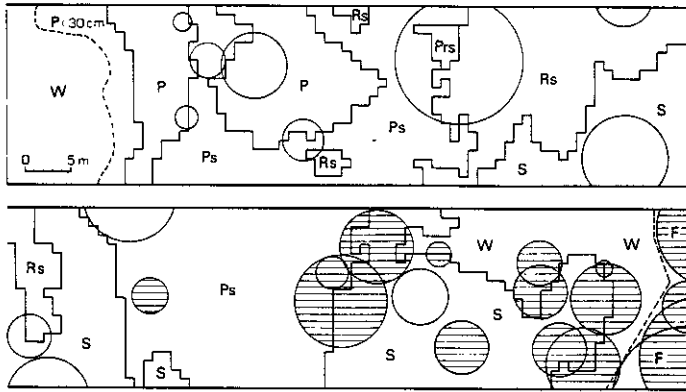


Fig. 1. Floating meadow. Distribution of aquatic plants. *P* *Paspalum repens*, *S,s* *Salvinia auriculata*, *R,r* *Reussia rotundifolia*, *W* open water, *F* inundation forest. Circles: leafy trees (hatched), leafless treetops (bare) (further explanations, see text)

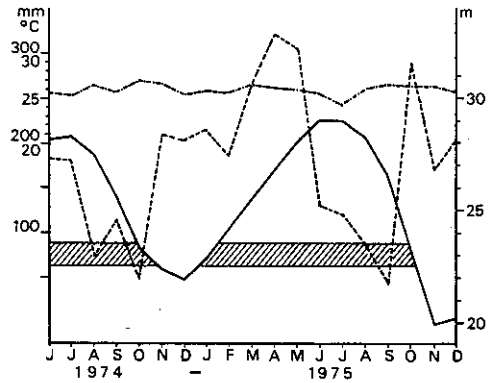


Fig. 2. Mean monthly air temperature (—), monthly precipitation (---) near Manaus. Fluctuation of the Rio Negro water level at Manaus (—). Hatching: vegetation period of floating macrophytes at the SW end of Lago Janauari

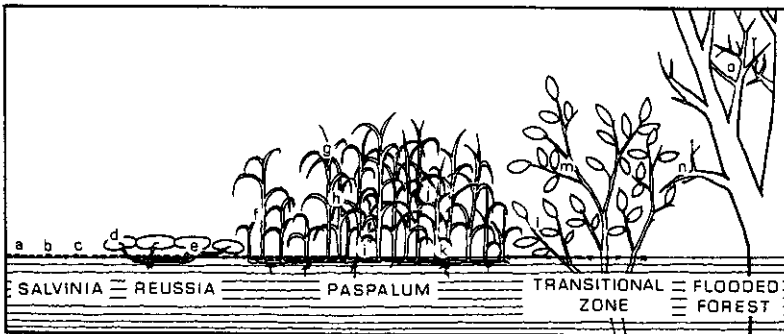


Fig. 3a-o. Calling positions of 15 anuran species. a *Lysapsus limellus laevis*, b *Sphaenorhynchus carneus*, c *S. dorisae*, d *Hyla rossalleni*, e *S. aurantiacus*, f *H. triangulum*, g *H. nana-like*, h *H. raniceps*, i *H. punctata*, j *H. lanciformis*, k *Leptodactylus wagneri*, l *H. haraldschultzi*, m *H. boesemani*, n *H. egleri*, o *H. boans*

thorhiza, *Neptunia* sp., *Phyllanthus fluitans*, and *Azolla* sp. were represented only minimally within that group. *Pistia* sp., abundant in floating vegetation along the banks of white-water rivers, was comparatively scarce, probably due to the slight current at the study area. *Reussia rotundifolia* and a few sporadically distributed *Eichhornia crassipens* represented the second category ('*Reussia* vegetation'), consisting of horizontal and vertical plant structures up to a height of about 40 cm. In the third category, formed by grasses ('*Paspalum* vegetation'), vertical structures dominate. *Paspalum repens* was by far the most abundant species. *Echinochloa polystachya*, very common in nearby areas, represented less than 10% of the grasses found in the measured section. The inundation forest with an average canopy height of about 20 m represented a barrier to the floating vegetation. Probably insufficient light conditions at the water surface prevented the aquatic macrophytes from growing within the adjacent flooded forest. A transitional zone was formed by scattered trees rising up to a maximum height of about 6 m above high-water level. An average water depth of 6 m was found in the measured section. At the study area aquatic plant populations started to develop in December 1974 and became dry during October 1975, according to the data on the fluctuations of the water level given in Figure 2.

Results

With the exception of *Lysapsus limellus laevis*, which could be heard regularly during the day after rainfalls, all species showed exclusive nocturnal activity. Calling activity started about dusk and ended generally between 0100 and 0300 hours. Once the calling stations were occupied, the males started to call without normally changing their positions. In a few species intraspecific territorial acoustic behaviour was observed (Hödl, in preparation). By then conspecific males often started to change their calling stations, and remarkable locomotorial activity arose. Breeding periods overlapped broadly (Table 1). At the study

Table 1. Breeding activities in 15 species of frogs. Observation of calling males (○), amplexing pairs and/or gravid females (×)

	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.
<i>Lysapsus lim. laevis</i>	○	○	—	○	○	○×	○×	○	○
<i>Leptodactylus wagneri</i>		○	—	○	○×	○×	○×	○	○
<i>Sphaenorhynchus carneus</i>	○	○	—	○×	○	○×	○×	○×	○×
<i>S. dorisae</i>	○	○×	—	○×	○	○×	○	○	○
<i>S. aurantiacus</i>	○	○×	—	○×	○	○×	○	○	
<i>Hyla nana-like</i>	○	○×	—	○×	○×	○×	○	○	○
<i>H. haraldschultzi</i>			—	○	○	○	○×	○×	○
<i>H. rossalleni</i>			—	○				○	○
<i>H. triangulum</i>	○	○	—	○×	○×	○×	○	○	○
<i>H. egleri</i>			—			○×	○×	○×	○×
<i>H. boesemani</i>			—		○	○×	○	○	
<i>H. punctata</i>	○	○	—	○×	○	○×	○×	○×	○
<i>H. raniceps</i>	○	○	—	○	○	○×	○×	○×	○×
<i>H. lanciformis</i>			—		○	○	○	○×	○×
<i>H. boans</i>	○	○	—	○	○	○	○	○	○

area all species besides *Hyla egleri* and *Hyla rossalleni* were found synchronically calling from April until July.

Calling Site Segregation

The calling positions of 15 species can be identified with certain physiognomic types of vegetation (Fig. 3). Individuals of *Lysapsus limellus laevis* called exclusively at water level on *Salvinia* vegetation. The same plants were used as calling positions by *Sphaenorhynchus carneus* and *S. dorisae*. If disturbed the latter species usually sought shelter under the leaves of nearby *Reussia* or any other protective vegetation. Calling males of *Hyla rossalleni* perched on either *Salvinia* or *Reussia* vegetation. Stems of aquatic plants within clear *Reussia* populations were the dominant calling positions of *S. aurantiacus*. This species usually called from places 2 to 10 cm above water level. Grasses covered the calling stations of 6 species. Fields of young *Paspalum repens* with *Salvinia auriculata* scattered between were used predominantly by *Hyla nana-like* and *H. triangulum*. The latter also perched on *Reussia* vegetation. Dense aggregations of aquatic plants were the favoured calling sites of *Hyla punctata* (*Paspalum*, *Reussia*) and *Leptodactylus wagneri* (*Paspalum*). They called from very secluded spots at water level. *H. raniceps* generally perched at about half height of the grasses, mainly at the edge towards open water or towards vegetation of

Table 2. Calling sites and mean SVL (snout-vent length in mm) of 15 anuran species

Species preference	Aquatic		Semi-terrestrial		Arboreal
	<i>Salvinia</i>	<i>Reussia</i>	<i>Paspalum</i>	Transitional zone	Flooded forest
Mean SVL (♂♂) (N=10)					
16.8–20.4	<i>S. carneus</i> (16.8) <i>L. lim. laev.</i> (20.1)	<i>H. rossalleni</i> (20.4)	<i>H. nana-like</i> (17.4)	<i>H. haraldsch.</i> (19.5)	
25.4–27.9	<i>S. dorisae</i> (27.6)	<i>H. triangulum</i> (25.4)		<i>H. egleri</i> (27.9)	
33.7–34.3		<i>S. aurantiacus</i> (34.2) <i>H. punctata</i> (34.3)	<i>L. wagneri</i> (33.7)	<i>H. boesemani</i> (33.8)	
48.8–103.0			<i>H. raniceps</i> (48.8) <i>H. lanciformis</i> (70.0)		<i>H. boans</i> (103.0)

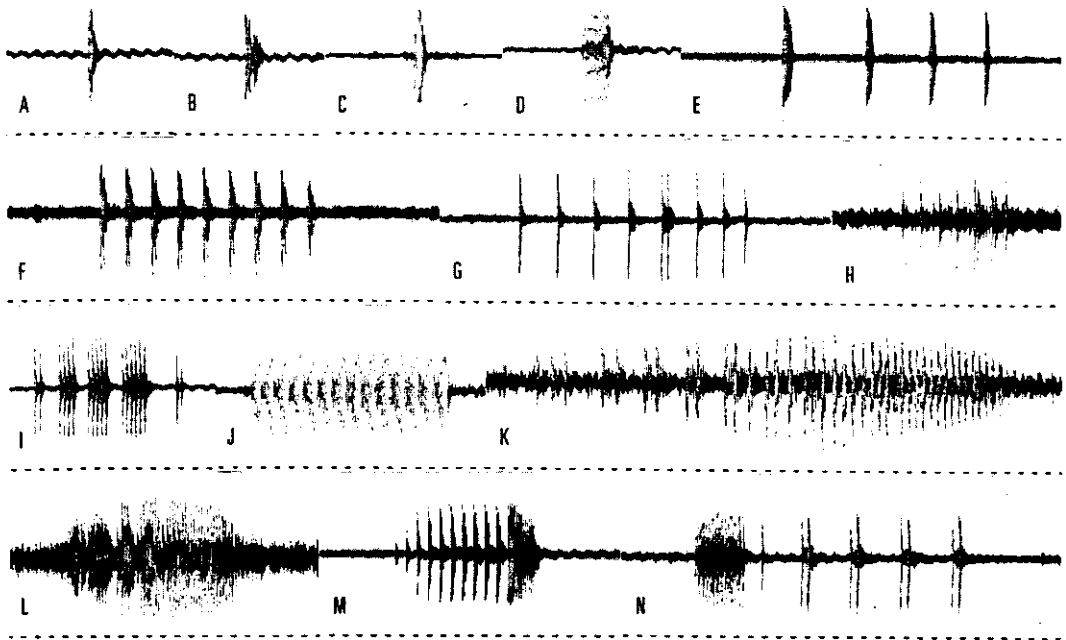


Fig. 4 A-N. Mating calls (oscillograms) of 14 species of frogs. A *H. nana-like*, B *S. carneus*, C *L. wagneri*, D *S. aurantiacus*, E *S. dorisae*, F *H. punctata*, G *L. limellus laevis*, H *H. raniceps*, I *H. triangulum*, J *H. boesemani*, K *H. boans*, L *H. lanciformis*, M *H. haraldschultzi*, N *H. rossalleni*. Time marking: 50 cps

minor density. *H. lanciformis* called at a height of 0.5 to 2 m, sitting either on strong grasses or on treetops rising just above the water level amidst a *Paspalum* field. The upper third region of grasses was the typical calling station of *H. nana-like*, the most abundant species found at the study area. Not all of the acoustically perceivable species had their calling positions within the floating vegetation. *H. haraldschultzi*, *H. boesemani*, and *H. egleri* were commonly found calling in the transitional zone, perched on leafy branches. In contrast to all other frogs, *H. egleri* always was observed calling in a downward position. In a few exceptional cases, *H. boesemani* and *H. haraldschultzi* could be found in *Paspalum* fields without any trees nearby. Croaks of *H. boans* could be heard from a distance up to 200 m or more. All 24 calling individuals observed in this study were found at the edge of or within the inundation forest, perched on nearly or completely leafless branches at a height of 1 to approximately 4 m above water level. During the high-water period, the grossly estimated density of Anurans found within the study area was about 1 individual/m². Table 2 shows that the calling sites of several species with males having about the same snout-vent length are separated from each other. Species preference for aquatic, semi-terrestrial, and arboreal environments is assumed to be responsible for spatial separation. The species-specific differences in calling sites used

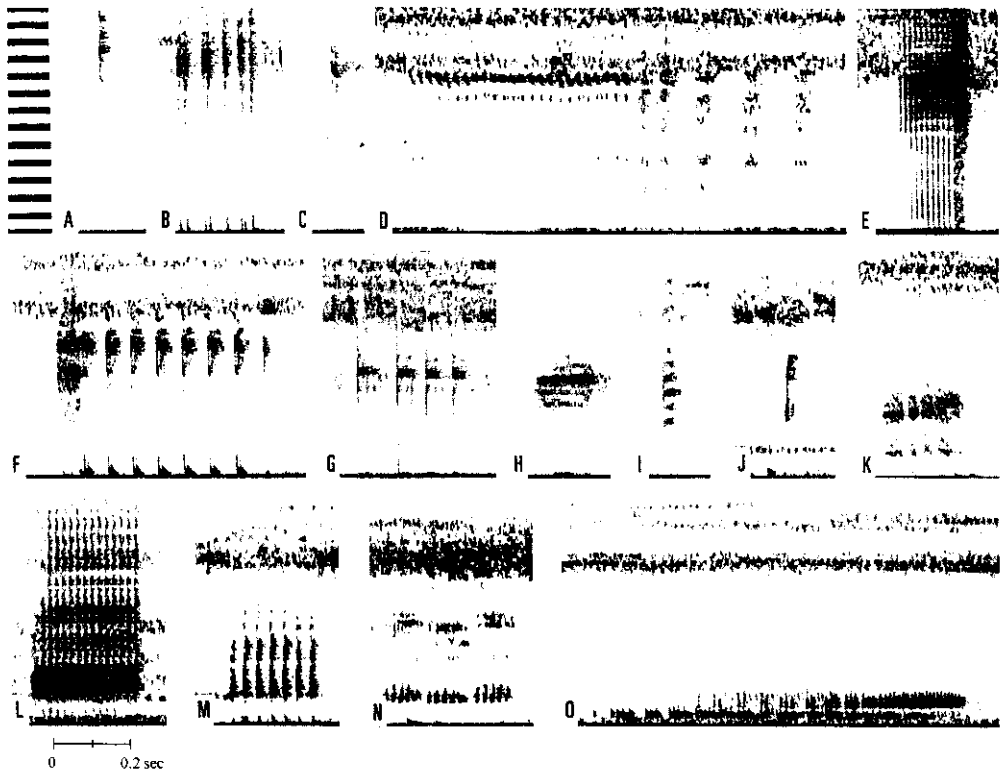


Fig. 5A–O. Mating calls (sonagrams) of 15 species of frogs. A *S. carneus*, B *L. limellus laevis*, C *H. nana-like*, D *H. egleri* (primary note + 5 secondary notes!), E *H. haraldschultzi*, F *H. rossalleni*, G *S. dorisae*, H *H. triangulum*, I *S. aurantiacus*, J *L. wagneri*, K *H. lanciformis*, L *H. boesemani*, M *H. punctata*, N *H. raniceps* (3 calls!, 2 individuals), O *H. boans*.

(Background noise derives from insects and distant frog choruses). Spectral markings: 500cps (0–6500 cps)

by the males cannot be explained by their weight and size alone. Whereas it is obvious that *Hyla boans* cannot perch on *Salvinia* vegetation or slender grasses, *Sphaenorhynchus carneus*, *Hyla nana-like*, and *Hyla haraldschultzi* for example could, according to their size, easily share the same calling sites. At the beginning of the development of aquatic macrophytes, when local densities of calling males sporadically reached up to 4 individuals/m² or more, calling positions were not as distinct as during the high-water period. Yet calling sites were characteristic for each species throughout the observation period.

Mating Call Structures

The mating calls of 13 species examined in this study are very distinctive and easily distinguished by the human ear. Only the calls of *Sphaenorhynchus carneus* and *Hyla nana-like* are difficult to differentiate from each other. Possible variations in call structures due to differences in temperatures, as is known for

Table 3. Mean snout-vent length (SVL) of males and mating call characteristics of 15 anuran species

	1	2	3
Pseudidae			
<i>Lysapsus</i>			
<i>L. lim. laevis</i>	20.1 (18.7–21.8)	4878 (4500–5600)	47/chorus
Leptodactylidae			
<i>Leptodactylus</i>			
<i>L. wagneri</i>	33.7 (31.2–36.9)	3162 (2800–3600) +1700–2200	77/chorus
Hylidae			
<i>Sphaenorhynchus</i>			
<i>S. carneus</i>	16.8 (15.2–18.4)	5611 (5300–5800)	31/chorus
<i>S. dorisae</i>	27.6 (25.6–29.3)	2893 (2500–3000)	36/chorus
<i>S. aurantiacus</i>	34.2 (32.0–41.6)	2346 (2100–2600)	33/13
<i>Hyla</i>			
<i>H. nana-like</i>	17.4 (16.0–18.4)	4835 (4500–5600)	159/chorus
<i>H. haraldschultzi</i>	19.5 (17.9–22.0)	4183 (3800–4600)	7/5
<i>H. rossalleni</i>	20.4 (19.4–22.6)	4025 (3800–4300)	5/2
<i>H. triangulum</i>	25.4 (23.2–28.3)	2830 (2200–3200)	28/11
<i>H. egleri</i>	27.9 (26.3–30.0)	4500 (4200–4800)	8/2
<i>H. boesemani</i>	33.8 (31.7–35.4)	1197 (900–1800)	26/3
<i>H. punctata</i>	34.3 (31.2–38.6)	920 (800–1400)	39/chorus
<i>H. raniceps</i>	48.8 (43.2–54.7)	879 (700–1200) +2600–3200	61/chorus
<i>H. lanciformis</i>	70.0 (66.8–76.1)	2087 (1800–2500)	31/chorus
<i>H. boans</i>	103.0 (84.1–110.6)	376 (200–700)	13/3

1 SVL (mm), $n=10$. 2 dominant frequency, absolute ranges of dominant frequency bands (cps). 3 n calls/individuals. 4 call duration (ms). 5 inter-call intervals (s). 6 pulse repetition rate (pulses/s). 7 notes (separated pulses)/call. 8 n , calls/individuals. 9 call rate (calls/min), $n=1$. 1, 4–7: ranges given below means (further explanations, see text)

* Call duration given for calls consisting of a single note

4	5	6	7	8	9
277 (164-348)	1.50 (0.37-2.99)	33.3 (25-54)	9 (6-12)	33/6	33
24 (18-32)	0.27 (0.19-0.39)		1	50/7	199
16 (8-28)	?		1	31/chorus	?
355 (152-502)	2.49 (1.86-3.25)		3.8 (3-6)	21/4	25
40* (32-46)	2.04 (0.87-3.33)		1.3 (1-2)	33/13	25
12 (9-16)	0.36 (0.25-0.92)		1	35/3	159
222 (198-248)	1.01 (0.94-1.66)	60.9 (53-65)	comp. call	23/5	48
399 (172-576)	2.13 (0.78-4.66)		comp. call	15/2	24
211 (140-310)	0.34 (0.26-0.53)	122.9 (98-150)	2.3 (1-5)	28/11	28
1580 (840-1850)	ca. 10.2	41.0 (38-43)	comp. call	8/2	6
277 (190-385)	1.72 (0.64-3.82)	48.8 (41-56)	1	26/3	31
326 (160-476)	1.06 (0.54-1.95)	27.4 (24-30)	9.6 (5-15)	32/5	43
127 (92-164)	0.63 (0.31-0.97)	66.6 (57-80)	8.9 (6-11)	22/3	76
238 (163-320)	0.43 (0.16-0.56)	28?	1	29/3	70
810 (650-1190)	3.48 (2.28-4.70)	60.9 (54-66)	1	19/3	14

several other Anuran species (Bellis, 1957; Schneider, 1974), were not treated in this study, because of nearly constant temperature conditions. All of the calls analysed in this study were recorded at temperatures of 22.5–25.3° C for air and 26.8–28.3° C for water, measured at 5 cm below the surface.

Oscillograms of the mating calls of 14 species are presented in Figure 4. Due to intensive background noise in the recordings of *Hyla egléri*, temporal characteristics of their calls had to be measured by audiospectrograms (Fig. 5D). The mating calls of 5 species are untrilled and consist of either a single note (Fig. 4A–D) or a group of well-separated notes (Fig. 4E). Oscillograms of *Hyla punctata*, *Hyla raniceps*, and *Lysapsus limellus laevis* reveal short series of quickly repeated notes. These calls may be considered as transitions from separated notes to trills. Trilled notes, formed by a series of connected pulses, are found in the calls of 7 species (Figs. 4 I–N and 5D). In *Hyla triangulum* groupings of short-pulse series are sometimes found within a single call. The structure of the connected pulses in the recordings of *Hyla lanciformis* is variable. The recorded calls of *Hyla egléri*, *Hyla haraldschultzi*, and *Hyla rossalleni* consist of two different kinds of notes and are therefore considered to be compound calls (cf. Duellman, 1970).

Various temporal characteristics are compared in Table 3. Variations in the number and duration of notes result in remarkable differences in the duration of the calls, which vary from 0.012 s in *Hyla nana-like* to 1.58 s in *Hyla egléri*. Inter-call intervals seem to be correlated with the duration of the calls. Brief calls, like those of *Hyla nana-like* and *Leptodactylus wagneri*, are repeated up to about 30 times faster than the long calls of *Hyla boans* or *Hyla egléri*. Pulse rates are given for calls formed by a series of quickly repeated or connected pulses. They range from 27.4 pulses/s in *Hyla punctata* to 122.9 pulses/s in *H. triangulum*. The call rate (calls/min) is given for only one individual of each species. These data derive from males calling continuously over a period of at least one minute. Individuals calling with approximately constant pauses between calls over a period of 1 min could be observed in 12 species. Due to the regular occurrence of short-call series with an average of 4.4 calls in *H. triangulum* and 5.2 calls in *H. lanciformis*, the observed call rate of these two species is not directly related to the given inter-call intervals. In the recorded choruses of *Sphaenorhynchus carneus*, individuals could not be separated. Therefore no data of the call rate and inter-call intervals can be given for this species.

The mating calls show striking differences in the distribution of energy through the frequency spectrum. In the calls of several species sound energy is continuously spread over a wide range of the frequency spectrum, yet species-specific peaks are distinguishable (Fig. 5). The mean dominant frequency varies between 5611 cps in *Sphaenorhynchus carneus* and 376 cps in *Hyla boans*. Dominant frequency appears to be somewhat related to body size (cf. Blair, 1956). Small species generally have a higher frequency than larger ones (see Table 3).

Discussion

In 15 Central Amazonian species of frogs breeding synchronically at the edge of or within floating meadows, distinct differences between species-specific

acoustic behaviour can be found. Structural differences of the mating calls together with calling site partitioning are assumed to be of prime importance in species recognition and thus may represent an efficient mechanism for preventing mismating.

Distinct calling sites of males may play a certain role in reproductive isolation, if the assumption of a corresponding preference for environmental structures in conspecific females is accepted. Arboreal forms, aquatic types, and species calling in *Paspalum* fields are fairly separated. Species sharing identical calling sites, however, can hardly be reproductively isolated through slight differences in their preference for specific calling positions. Mating calls obviously appear to be the most important premating reproductive isolation mechanism between species found within the same type of vegetation. Nineteen gravid females showing positive phonotaxis towards conspecific calling males of 7 different species (*Sphaenorhynchus dorisae*, *Hyla triangulum*, *H. punctata*, *H. raniceps*, *H. nana-like*, *H. boesemani*, and *H. haraldschultzi*) could be observed under natural conditions. In the most striking observation, a female of *H. raniceps* approached a conspecific calling male over a distance of about 8 m within a dense *Paspalum* field. No noticeable reactions could be seen towards synchronically calling individuals of *H. nana-like*, *H. triangulum*, *H. punctata*, and *Leptodactylus wagneri*, which were passed by sometimes less than 30 cm. After tactile contact with the mate, the male stopped calling and amplexus followed immediately. The behaviour of the other mates was similar, except that the observed distances of the approaching females were less than 2 m.

As shown in Figure 4 and Table 3 the calls of most species are sharply differentiated in several temporal features, such as duration, pulse rate, inter-call intervals, and pattern of notes. Yet it is impossible to differentiate between particular species from general recordings of the chorus from the floating meadow Anuran community by means of oscillograms. Temporal patterns of synchronically calling frogs overlap considerably and mask each other. A species-selecting mechanism in the auditory system, based exclusively on temporal information, would normally fail to recognize species-specific calls within a continuous medley of various notes. Only calls emitted by nearby individuals that stand out against the environmental noise level could be of communicative value. A selection over distances with several individuals of other species calling between would be impossible on temporal differentiation alone.

Although most mating calls differ greatly in their spectral features, overlapping of dominant sound energy occurs even within some of the species preferring identical calling sites (Fig. 6). Identification mechanisms selectively tuned to species-specific spectral energy without the ability to differentiate between distinct temporal patterns might be able to register whether specific bands of sound energy are 'occupied' or not. Differentiation between two or more species sharing the same emphasised frequencies would be impossible on this basis.

Electrophysiologic studies of the auditory nervous system in several Anurans show striking correspondence with spectral and temporal patterns of species-specific calls (Capranica, 1976). In the cricket frog, *Acris crepitans*, the auditory nervous system can be tuned even to local dialects (Capranica et al., 1973). With an assumed species-specific selective sound detector, based on a combina-

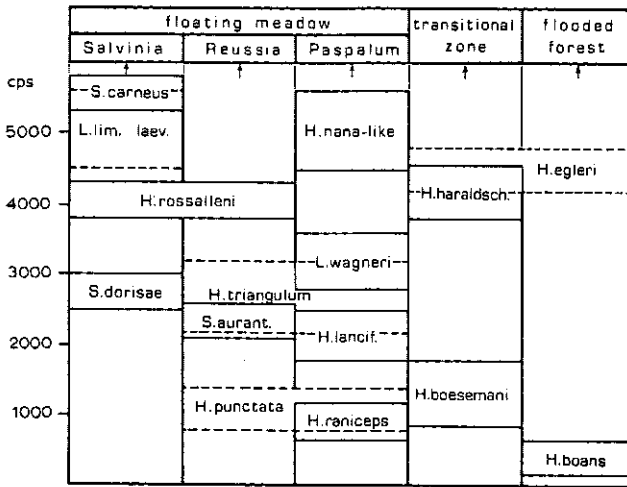


Fig. 6. Calling sites and dominant frequency ranges of 15 anuran species

tion of spectral and temporal properties, each species should be able to differentiate its specific call from all other environmental sounds.

The only difficulties might occur in the differentiation of the vocalisations between *H. nana-like* and *S. carneus*. Their absolute dominant frequency ranges overlap, and gross differences between temporal characteristics could not be found. A high call repetition rate, as is known for *H. nana-like*, is assumed in *S. carneus*, too, even though it could not be measured accurately. Goin and Layne (1958) describe the call of its synonym *Sphoerohyla habra* (see Duellman, 1974) as a high, thin rapidly repeated 'kik-kik-kik'. Differences between calling sites possibly play a significant role as premating isolation in these two sympatric species.

In all other species, spatial separation strongly reinforces the function of the mating call as a primary species identification signal. Due to differences in calling sites, dominant frequency ranges of 11 species are separated within their immediate acoustic environment. Only 4 species overlap in dominant frequency spectra with other species sharing their specific calling sites (Fig. 6). The calls of these species, however, are strongly differentiated in their temporal structures. At least two of the temporal variables given in Table 3 differ between species showing gross similarities in their emphasized energy bands.

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