VOCALIZATIONS OF PRIMARY FOREST FROG SPECIES IN THE CENTRAL AMAZON.

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SUMMARY

The calls of 18 species of Amazonian forest frogs were recorded in 3 localities: the Tapajos National Park near Itaituba, the Reserva Ducke near Manaus, and the INPA-WWF reserves near Manaus. Structural and time parameters and sonographs of these calls including previously undescribed vocalization by 10 species are presented. Unlike open habitat species, several forest frog species characteriscally demonstrated one or more of the following temporal parameters: very low call rates, sporadic intervals, infrequent nights of calling and synchronized chorusing. It is hypothesized that predation has influenced the evolution of vocal behaviour in Amazonian forest frogs.

INTRODUCTION

Frogs have been collected in the Amazon by naturalists for more than a century. In recent times, Lutz & Kloss (1952), Heyer (1976; 1977), Crombie (1979) and Hodl & Zimmerman (in preparation) have collected frogs extensively in the Brazilian Amazon. The taxonomy of many species of Amazonian frogs is known, although the geographical distribution of several species is less well known. Also, the calls of only a few Central Amazonian species have been completely described. Calls of some Amazonian frogs species were analyzed spectrographically by Duellman (1970; 1978) (mainly hylids); Schluter (1979; 1980) (hylids and microhylids); Heyer (1978; 1979) and Straughan & Heyer (1976) (leptodactylids). Hödl (1977) analysed the calls of 17 species of Central Amazonian floating meadow frogs (mostly hylids). Hodl's study was the only one to characterize the acoustics of a single Central Amazonian anuran community and presented detailed analyses of each species call measured from more than only one or two individuals.

During a survey of forest anura inhabiting the forest reserves of the Instituto Nacional de Pesquisas da Amazonia (INPA) and World Wildlife Fund (WWF) - U.S. between February and July, 1980, the calls of 14 frog species were recorded. Additional calls

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from the some of the same species were recorded in the Tapajos National Park near Itaituba in 1978 and in the Reserve Ducke near Manaus in 1978. The study reports the initial acoustic results obtained in a herpetological investigation in the INPA-WWF reserves and consititutes part of a larger project entitled, "Mininum Critical Size of Ecosystems" (see Lovejoy & Oren, 1977; Lovejoy, 1980). Anuran acoustic information in the reserve was obtained in order to:

1. Describe vocalizations by all species in the INPA-WWF reserves to be used as an aid to the survey. Calling frogs which are hidden or inaccessible can be easily and precisely identified.
2. Assist in behavioural studies involving responses to taped calls.
3. Characterize patterns of vocalization used by the frogs in the primary forest in order to compare these calls with those of frogs in open habitats or disturbed forest habitat.

MATERIALS AND METHODS

Recordings were obtained from 19 Amazonian species (Table 1). Most (14) were recorded in the INPA-WWF primary forest reserve but additional species and populations' were recorded in the Tapajos National Park (9 species) and the Reserva Ducke forest (8 species) (see Figure 1). Recordings in the Tapajos National Park were obtained between late August and mid-September or between mid-October to mid-December, 1978. Recordings and observations were made from July through October, 1978. The methods involved walking access, boundary, and transect trails. The position and locality of individuals were noted with respect to their height from the ground, microhabitat , and approximate position on the grid of trails which were spaced 1 Km apart within a particular reserve. Calling individuals were recorded and captured. Details of the species survey are reported elsewhere (Zimmerman, 1982 and in prep). Specimens are deposited in the collection of the Museu de Zoologia, Universidade de São Paulo(MZUSP) Brazil.

ACOUSTIC ANALYSES

Frog vocalizations were recorded with a Uher 4000 Report L tape recorder at a tape speed of 9.5 cm/sec and with a Uher M 517 microphone. Calls were analyzed from sonograms made on a Kay Elemetrics Model 7030A sonograph at normal recording speed and narrow (45 Hz) and/or wide (300 Hz) filter bandwidth setting. Plots of instantaneous frequency versus amplitude (sections) were made with the sonograph when emphasized (or dominant) frequencies in a call were not obvious from distinct contrast differences of the markings on the sonogram. Sonograms were measured using digitizer-computer systems with programs written by the junior author and J.R. Malcolm of the University of Guelph. The same computer system is used for chromosome analyses (see Green **et al.**, 1980).

Terminology:

a) Frequency modulation (FM): - Defined as a change in frequency with time as seen on narrow-band sonograms of a call (Fig. 2b, 2c.). Frequency modulation has rise time (the time taken for the frequency to reach its maximum value) and/or decay time (the time taken for a frequency to fall from a maximum to a minimum value) (Fig.2c). The slope is the vertical distance of the frequency modulation divided by the horizontal distance (Fig. 2c.).

b) Amplitude modulation (AM): - Discrete, temporal discontinuities which appear, sometimes as "streaks", on the sonogram using either narrow or wide filter bandwidths (Fig. 2a). Differentiation between AM and FM calls were determined by the sound spectrograph such that temporal resolution was limited to the narrow band filter (about 25 msec).

c) Pulses: - Described as the shortest cycle of amplitude modulation of a frequency or a frequency range (Straughan & Heyer, 1976) (Fig. 2a). When pulses are regularly periodic, a pulse repetition rate may be estimated.

d) Harmonics: - Frequency bands which are equally spaced apart on narrow band sonograms (Fig. 2d, 2e).

e) Emphasized Frequency: - The frequency range, in narrow band sonograms, which contains the greatest amount of energy (Fig. 2e).

f) Broadband Noise: - The pattern on the sonogram is distributed over a relatively wide frequency range (Truax, 1978) (Fig. 10g). The vibrations are non-periodic.

g) Notes: - Single sounds (pulsed or not) of at least 0.05 secs duration and occur 0.05 secs or more apart from other discrete sounds. Notes represent single contractions of the thoracic musculature (Fig. 15).

h) Call: - The longest, sequence of sound emitted during a vocalization by a frog . Usually, a call consists of either one note (Fig. 5);more than one note emitted in defined, temporal patterns (Fig. 3); or sequences of different kinds of notes(Fig. 14). The definition is arbitrary because there is a continuum of variables which compose a call. For example, a single note call without temporal discontinuity is no different than a pulse, but it is arbitrarily designated a "call" because of its duration (Straughan & Heyer, 1976). It may be difficult to identify a repeated pattern of sound with the total vocalization of a frog (e.g. complex calls of **Hyla geographica**, type B calls of **Phrynohyas resinifictrix**, territorial calls of **Eleutherodactylus fenestratus**) (Fig. 17). In such cases, "call" is a general term which refers to a train of vocalizations.

i) Tonal Call: - A call in which the frequency range, at any instant, is no greater than about 350 Hz (Fig. 2c. 2d.).

j) Advertisement Call: - A call usually produced by a breeding male and, according to Wells (1977a), probably serves to attract conspecific females to calling males and to announce territorial occupation to other males (all Figs. except 12d,13b, 17,18).

k) Territorial Call: - The call produced by a resident male in response to an advertisement call received above a critical threshold of sound intensity (Littlejohn, 1977). In this study, territorial calling is considered to be any vocal response which differed from the advertisement call which was evoked by playing back a conspecific advertisement call to an individual (Fig. 13b, 17, 18).

l) Chorus: - Rhythmical interactions, or phonoresponse, of calls by neighbouring calling males (Alexander, 1975).

m) Synchronized Chorus: - A chorus in which the calls of one male seem to stimulate calling by other males resulting in considerable overlap of calls (Wells, 1977b) or sequential emission of calls. All calling by group members occurs with relatively short periods separated by relatively silent periods.

RESULTS

The acoustic analyses are presented for each species which was observed in the INPA-WWF reserve areas, Tapajos National Park, and the Reserve Ducke. Information obtained from each species is presented below, and summarized in Table 1.

DENDROBATIDAE

Phyllobates femoralis

P. **femoralis** called most often in the late afternoon as reported by Duellman 1978 in Ecuador. The advertisement call of P. **femoralis**, recorded in the Reserve Ducke , consists of four evenly spaced, frequency modulated, notes (Table 1; Fig, 3). The last three notes in the series were similar with respect to frequency range, rise time, slope of frequency modulation, and duration (Table 1) but the first note was somewhat variable with respect to these parameters. Hodl (pers. comm). suggests that the note structure of the advertisement call is geographically variable but exhibits little variation within or between individuals in the same region. Meede (1980) discussed two distinct calls given by captive P. **femoralis**. The "normal" call, described by Meede (as type c) corresponds to the advertisement call in Table 1. Meede's second (or A) call type, described as a soft, uniform sounding call emitted by the male in close proximity to a female, is probably the courtship call which occurs in several species of Dendrobates and Phyllobates (Wells, 1977a). This call was not heard in the present study. P. **femoralis** is very responsive to play-back experiments and usually aproach a tape recorder playing the conspecific advertisement call.

HYLIDAE

Centrolenella oyampiensis

C. **oyampiensis** was frequently heard in the INPA-WWF reserves but calling individuals were difficult to locate as individuals called sporadically and would cease calling when approached. The call energy fell in a frequency range of ambient insect noise which obscured calls on sonograms (Fig. 4). Measurements were restricted to obvious features such as frequency range and duration. The advertisement call does not appear to have a clear dominant frequency but the energy of some calls was increased at a mid-point of the frequency range (Table 1). Harmonics were evident in some calls (Fig. 4a) and may not have been resolved in other calls because of the intensity of the background noise (Figs. 4b). The advertisement call was usually emitted twice in rapid succession separated by long silent intervals. Less frequently, a single call was given. Synchronized chorusing was characteristic of this species at several sites.

Hyla boans

H. boans has two call types (A and B). Type A, the advertisement call, is most commonly heard in the dry season and in aggregations at breeding sites. Call Type B was analyzed by Hödl (1977) and involved solitary males calling in flooded forest(igapo) near Manaus between December and August. Hödl described this call as a long (mean duration of 0.81 sec), low-pitched (nean dominant frequency of 0.38 kHz), pulse train(mean pulse repetition rate of 60.9 pps). Call type B of **H. boans** is fairly similar to call type A of **Osteocephalus taurinus** (Table 1; Fig. 9). **H. boans** has only been observed to breed during the dry season and is not known to oviposit in igapo. Thus, the function call Type B is not presently understood. Advertisement (Type A) calls were analyzed from recordings made of a single INPA-WWF individual (Fig. 5) and a chorus of individuals from the Tapajos National Park. This call was a highly stereotyped, pulsed , explosive burst ranging from 0.3 to 1.75 kHz (Table 1). Calls were initiated with two or three short (.02 to .03 sec) pulses which were slightly separated from the rest of the call (Fig. 5). The advertisement calls of **H. boans** described from Panama (Duellman 1970) and from Peru (Schluter, 1979) are similar in all respects to Brazilian Type A calls (Table 1).

Hyla geographica

Calls of **H. geographica** were soft and could only be heard within a few meters of the frogs, which usually called in small groups. Individuals produced a variety of low frequency, short and long sounds. The most consistent call, emitted by all individuls is considered to be the advertisement call and is designated call type A (Table 1;Figs. 6a, 6d, 6f). Call type A was a series of from three to nine short (mean 0.06 sec), similar pluse trains which followed one another at about 0.02 sec intervals. The final pulse train in a call was often the longest. A variety of other short sounds, described as " clucking and whimpering noises" by Lutz (1973), are here considered to be type

B calls and were usually interspersed with bouts of call type A. The only common feature among the type B calls was single pulsed bursts or notes comparable in duration and frequency range to single pulse trains of call type A but sometimes consisted of two or three narrow FM, harmonic, bands (Table 1; Figs, 6b,6c,6d,6e). Call parameters of **H. geographica** from the INPA-WWF area, the Tapajos National Park, and the Reserve Ducke were similar. Pulse rates varied among the calls from single individuals but, in general, tended to be very high (Table 1). Ecuadorian (Duellman, 1978) and Peruvian (Schluter, 1979) **H. geographica** do not appear to have type A calls in which the pulses occur in trains as they do in the Brazilian calls.

Hyla granosa

H. granosa was found to call in small groups. Individuals were difficult to locate as their calls were ventriloquial to the human ear. The call of **H. granosa** is a non-pulsed, pure tone which is emitted at irregular intervals (Fig. 6c, 7). All the calls had at least one harmonic containing slightly less energy than the emphasized frequency. There was no apparent difference between the INPA-WWF reserves calls and those recorded the Tapajos National Park (Table 1). Calls of H. **granosa** described by Schluter (1979) from Peru match those of the Brazilian populations. Duellman (1974) reports that the calls of this species from the Guianas and the Lower Amazon are also alike.

Hyla marmorata

Only one small chorus of H. **marmorata** was heard in the Tapajos National Park . Five or six members of this chorus called synchronously in short bouts and, in general, the calls of one individual would overlap the calls of other individuals. Call alternation between two individuals was heard on the banks of the Tapajos River. Solitary individuals were heard calling in the INPA-WWF reserves as well as in the Tapajos National Park. The advertisement call of H. **marmorata** has two, separated frequency ranges without a distinct harmonic frequency (Fig. 8). The call appears pulsed on wide band sonograms and is composed of closely spaced side bands on the narrow band sonogram. Call rates, especially of single calling individuals, were variable and irregular (Table 1 Fig. 8).

Osteocephalus taurinus

O. **taurinus** has two call types (A and B) which may represent two parts of a single compound call but the two call types were not always given together. Call type A is a low frequency, clearly pulsed call of long duration (Table 1; Fig 8a) and probably is the advertisement call. Call type B is much softer than call type A and is variable in structure but generally consisted of short pulses or notes emitted in trains (Table 1; Fig. 8b). Duellman & Lescure (1973) described two call types from Ecuadorian O. taurinus and two call types were reported by Schluter (1979). Call type A in the present study would correspond to Schluter's call type A and Duellman and Lescure's call type B. In general, the call parameters provided by Duellman & Lescure (1973) and Schluter (1979) are similar to those provided in Table 1 but the Ecuadorian O. **taurinus** seems to have a shorter type A call with an increased pulse rate (Duellan & Lescure , 1973; their call type B). Call type B (Duellman and Lescure's call type A) varies considerably both within and between individuals with respect to call length, frequency modulation, harmonics, and pulses but always contains a series of short (about 0.05 sec) notes. In choruses of O. **taurinus** in the INPA-WWF reserves, call type A was always the dominant call which was followed or not by various type B calls. This species has been reported to call in small to large, highly synchronized choruses (Bokermann, 1964; Hodl, pers. comm.) such that there is a high degree of call overlap among individuals.

Osteocephalus sp.

This species produced a broadband unmodulated call which was usually initiated with two or three short (.02 to .04 sec) pulses (Fig. 10). Call variation was evident within an individual (Fig. 10a to 10e) and between individuals (Figs. 10a to 10g) in the INPA-WWF reserves and the Tapajos National Park. Call variability included the presence and the number of preliminary pulses, call duration, intercall intervals , emphasized frequencies, frequency modulated harmonics. The call was usually emitted one to four times in succession (call series) sporadically in the day or the night although calling was more frequent at night (before 2330 h) and during wet weather. Intervals between calls, or call series, varied from several minutes to hours and only rarely did an individual call at regular intervals. This species may have more than one structural call type but it was not possible to identify obvious repeated patterns in the calls. The call of this species appears to be similar to that described by Schluter (1979) for **O. leprieurii** from Peru with respect to structural and temporal patterns although Schluter did not report pulses in the call of **O. leprieurii**. Basically, **O. leprieurii** has a call which could be characterized by the parameters presented in Table 1 for **Osteocephalus sp.** Such information could be useful in future taxonomic considerations of these species.

Phrynohyas resinifictrix

Individual P. resinifictrix were heard calling in the same trees over the six months of this study and the call has been heard in all months of the year (Hodl, pers comm.; present study). Calls are loud and single individuals can be heard, depending on the terrain, from a distance of 250 to 500 meters in the forest and from a distance of about one kilometer from the forest edge across open areas. Calling usually commenced one to two hours after dusk (about 2000 hr) and continued into the early hours of the morning. Calling individuals were generally widely spaced (more than 200 meters apart) and usually only one individual could be heard calling at any one time. P. **resinifictrix** also produces two distinctive call types. The advertisement call (call type A) (Figs. 11a, 11b.) was the most common vocalization and consisted of a series of one to six calls (mean intercall interval in the call series, 51 sec.) separated by intervals of several seconds (mean 14.5 sec.). Certain frequencies or frequency ranges were emphasized in call type A but varied between the calls of different individuals and sometimes between calls of the same individual. Call type A demonstrated seven to 12 harmonic bands on narrow band sonograms. There was no apparent chorusing, alternations of calls, or other types of acoustic interaction associated with type A calling individuals. Rarely, a second call type (call type B) was emitted by individual P. **resinifictrix** (Fig. 11d). Call type B is a prolonged vocalization consisting of short bursts and low frequency, drawn-out "groans" (Fig. 11c) emitted in close proximity and synchronously with one or two other individuals producing similar calls. This acoustic interaction was observed on four separate occasions. Individuals, emitting call type B were about 10 meters from the forest floor in large trees but were within 3 meters of each other. Type B calls were emitted from both individuals for more than an hour. Generally, type B vocalizations are patternless, continuous transmissions of non-pulsed sounds which vary in duration and usually fall within the lower range of type A call frequencies. The only distinctive sound units in type B calls are prolonged, low frequency sounds (Fig. 11c, "groans" which ranged from 0.35 to 2.20 sec)and short (.05 to 0.25 sec) bursts or trains of bursts (Fig. 11d). Bursts and "groans" sometimes immediately followed each other.

Phyllomedusa bicolor

P. **bicolor** call individually from 10 meters or more from the forest floor. They were heard calling during the entire study period but it is suspected that certain individuals remained silent for several nights to weeks. Intercall intervals often lasted many minutes to hours. The shortest intercall interval was 84.06 sec. Call rate varied considerably from the same tree (same individual?) on different nights. The usual call (call type A) of P. **bicolor** is a single, loud, explosive burst which can be heard over a considerable distance (100 meters or more) through the forest (Figs. 12a, 12b, 12c). The calls emitted by some individuals are distinctly pulsed and contain up to nine harmonic bands (Figs. 12a,12c) but other individuals do not appear to have either pulsed calls or harmonics (Fig. 12b). None of the calls have clearly defined fundamental frequencies although some of the harmonics may contain more energy. Sometimes,the single burst is followed by trains of softer bursts which may be part of a compound advertisement call. Compound advertisement calls are known in other Amazonian **Phyllomedusa**. These softer bursts were only successfully recorded from a single individual who emitted six to ten additional short, rapid (about. 08 sec intervals) notes in the "soft burst train"(about 0.75 sec in duration). A second call (Type B) was only heard from captive individuals, usually held in plastic bags. Call type B consists of from 5 to ten pulsed notes emitted in rapid succession (Fig. 12d) and is very similar to call type B of P. **tarsius**. Call type B differs from call type A primarily in call rate, amplitude modulation (pulsing), and harmonic structure.

Phyllomedusa tarsius

P. **tarsius** was found to call individually, separated by 100 to several hundred meters or in very small groups. The advertisement call (call type A) of **P. tarsius** in the INPA-WWF reserves is a single, pulsed note which is often followed by a second , shorter note (Table 1;Figs. 13a). The first note has an emphasized frequency range and the second, softer, note was similar to the first note but had a shorter duration, fewer pulses, and a narrower frequency range (Table 1). P. **tarsius** also produces a repeated burst call (call type B) which is probably a territoral call (Fig. 13b). Call type B was immediately elicited from individuals emitting call type A when call type A was played back to the calling individual from close proximity. The calling individual would continually emit call type B until the play back ceased. On one occasion, a playback of its own call induced a male to leave its perch and approach the tape recorder, a distance of 3 meters. A play back about 6 meters from another male did not induce him to move from his station but did elicit call type B. On several successive nights, two P. **tarsius** about 15 meters apart in small trees, away from breeding pools, called synchronously with call type B for more than an hour. Neither caller left his station during this time. Call type B consists of a series of five to eight pulsed notes emitted as two short pulse trains in rapid succession. Each pulse (about 0.03sec) appears equivalent to the second short note usually present in call type A. Each call is separated by silent intervals (mean 8.36 sec) (Table 1). Peruvian P. **tarsius** was also found to have two call types (Schluter, 1979) but neither call type is the same as that presented here from the INPA-WWF reserves. Indeed, Schluter's descriptions of call types A and B for P. **tarsius** from Peru match the two call types of **Phrynohyas resinifictrix** recorded in the INPA-WWF reserves. Also, the call parameters of **Phyllomedusa tarsius** in Table 1 do not closely match those obtained from Ecuadorian individuals by Duellman (1978). The call duration of the Ecuadorian frogs is about four times as long as that obtained from individuals in the INPA-WWF reserves.. It is possible that the calls of P. **tarsius**, unlike most other Amazonian hylids, are geographically variable.

Phyllomedusa tomopterna

P. **tomopterna** were found in small groups and chorused synchronously around a breeding pool. An individual gave one to three calls during a chorus of a few seconds closely following the call emitted by a neighbour. Calls of individuals followed each other sequentially so that, generally, the calls did not overlap. Each chorus was usually separated by intervals of many minutes. Call rates (also inter-chorus intervals) varied considerably between observation nights. The advertisement call of P. **tomopterna** consists of two, structurally dissimilar, notes (Table 1; Figs. 14a, 14b). The two notes were usually given in succession but sometimes they were produced independently (Fig. 14b). The first note was a "chuck" sound with ill-defined harmonics and usually possessing a high, but variable, pulse rate. The second, softer, note was a "whirr" sound with a narrower frequency range, well defined harmonics and pulse rate (Fig. 14a).

LEPTODACTYLIDAE

Adenomera andreae

Choruses of A. **andrea** were heard to chorus every dusk and dawn in the INPA - WWF reserves and in the Reserve Ducke. They also called after diurnal rain. The advertisement call is a short, stereotyped burst which is sometimes rather indistinctly frequency molulated (Table 1; Fig. 15). The call rate and intercall interval varied within individual calls and among individuals calling in a chorus. It is likely that the call rate has a territorial or inter-male competitive signal function (Wells, 1977b ; Greer & Wells, 1981) because calling A. **andrea** responded to play-back experiments with increased call rates.

Eleutherodactylus fenestratus

Choruses of E. **fenestratus** were heard every dusk and dawn throughout the forest and individuals called sporadically both during the day and at night. The advertisement call is a short, broad frequency band which always possessed distinct, evenly spaced (0.2 to 0.25 kHz) harmonic frequency bands (Table 1). When harmonic frequency bands were of differing intensities, the same two frequency bands (1.65 to 1.85 kHz and 2.7 to 3.76 kHz) were emphasized in all calls (Fig. 16). Variation was evident in call duration and in the number of harmonic frequency bands in the high frequency ranges. Measurement of the frequency range of the call was restricted to a range which encompassed at least 80 per cent of the energy as determined by the intensity of the bands on the sonogram. One individual had a third, clearly emphasized harmonic frequency band (6.56 to 7.62 kHz) (Fig. 16a). The advertisement call may be emitted in rapid succession(intercall interval of only 0.05 sec) such that it is difficult to distinguish whether the advertisement call is a single note with a very short intercall interval or whether the advertisement call contains one to three notes with a .05 sec internote durations. Some calls were clearly single note calls. In addition to the advertise - ment call, E. **fenestratus** produces a variety of other sounds which probably have a territorial function because they were only heard during male-male interactions and during play-back experiments (Figs. 17,18). Males are highly responsive to calls of conspecific males and would approach the tape recorder during play-back experiments. Three general sound types were identified from among the variable "territorial calls":

1) Rapid bursts - a staccato series of unstructured notes or bursts containing from three to nine notes in each series. Each note contained two areas of emphasized frequency in the same ranges as those in the advertisement call (Fig. 17f).
2) Single burst - variable pulsed sounds emitted singly and containing a few fairly distinct harmonic bands with emphasized frequencies in the same range as in the advertisement call. The harmonic bands were frequency modulated, having a steep, lingering decay (negative slope) (Figs. 17b to 17e).
3) Squeal - very clear, unmodulated harmonic bands with regular pulsing which was only recorded during a fight sequence (Fig. 18a). Structurally, this call is a prolonged advertisement call within a confined frequency range (1.49 to 3.59 kHz) but frequency range and call duration is variable. Very short (0.05 sec) "peeps" sometimes preceded a "squeal".

The highest band of emphasized frequency in E. **fenestratus** calls is lower than that of **Adenomera andreae** which calls during the same time and in the same areas as E. **fenestratus**. Also, a ubiquitous, ambient (insect) noise band is in a frequency range which is just above the lowest band of emphasized frequency in E. **fenestratus**. Thus, the two areas (harmonic frequency bands) in E. fenestratus appear in areas of the sound spectrum which is relatively free of ambient noise (Fig. 16b).

Leptodactylus amazonicus

The advertisement call of L. **amazonicus** consists of a single, pulsed, frequency modulated note which is emitted at regular, short intervals (Table 1; Fig. 19). Over a four month period in the INPA-WWF reserves, L.**amazonicus** was observed on the forest floor most nights. Aggregations of calling males were, however, only heard during three nights. The call parameters (Table 1) correspond to those reported by Heyer (1978) except that L. **amazonicus** from the Tapajos National Park have three to five fewer pulses per call.

Leptodactylus pentadactylus

In the INPA-WWF reserve and the Reserve Ducke, L. **pentadactylus** called individually near the mouths of burrows. The advertisement call of L. **pentadactylus** is a single, low frequency, unpulsed, slightly frequency modulated note (Table 1; Fig. 20) Call duration, slope and rise time of FM, and call rate varied between individuals (Fig. 20). Frequency parameters were also somewhat variable between individuals which may be due, in part, to size differnces between calling males. In some species, the emphasized frequency is negatively correlated to body size (Littlejohn, 1977). The advertisement call of **L. pentadactylus** appears to be geographically variable. Costa Ri can populations have pulsed, rather than unpulsed advertisement calls, with a mean pulse rate of 40 per sec (Straughan & Heyer, 1976) but other acoustic parameters are similar to those in Table 1. The fundamental frequency of one **L. pentadactylus** call from Ecuador was reported to be 3.3 kHz (Duellman, 1978) which is very high compared to mean values for the highest call frequencies in the present study or those obtained by Straughan & Heyer (1976), Rivero & Esteves (1969), and Fouquette (1960, cited by Straughan & Heyer, 1976) which were 0.94, 0.5, 0.5, and 0.45 kHz respectively.

Leptodactylus stenodema (?)

A frog, which was recorded in the INPA-WWF reserves, produced a call which was similar to, but different from, L. **pentadactylus**. The individual was not captured as it retreated down a burrow when it was approached. The call analyses of this vocalization (Table 1) is very similar to that proveded by Pyburn & Heyer (1975) for Colombian L. **stenodema**. The call is a single short (0.4 to 0.5 sec), frequency modulated note. The call contains a weak harmonic frequency band and the call rate is about 5.76 calls per min. These call parameters are very similar to those of **L.pentadactylus** (Table 1) but the presence of the harmonic frequency band may be a useful characteristic to distinguish between these two calls.

Leptodactylus wagneri

L. **wagneri** was found calling alone or in small groups. The advertisement call is short and unpulsed with a wide frequency range (Fig. 21). The energy in the calls *of INPA-WWF individuals was concentrated in two frequency ranges in the same time frame* (Table 1; Figs. 21a, 21c). A Tapajos specimen did not demonstrate similar energy divisions in its call (Fig. 21b). Occasionally the calls were slightly frequency modulated (Fig. 21a) having the highest frequency in the middle of the call and equal positive and negative slopes (approximately 1 and-1). The advertisement call of L. **wagneri** is geographically variable. Straughan & Heyer (1976) compared calls from Brazil, Venezuela, and Ecuador. Frequency ranges calculated in the present study (Table 1) are slightly lower than those obtained by Straughan and Heyer from their Brazilian specimen and two weak harmonic bands, noted by Straughan and Heyer, were not apparent in the call of L. **wagneri** from the INPA-WWF reserves or the Tapajos National Park. Advertisement calls recorded by Hodl (1977) in the floating meadow near Manaus were structurally similar to those analysed here (Table 1) but were shorter in duration and the emphasized frequency range was about 1 kHz higher.

MICROHYLIDAE

Synapturanus salseri

Densities of the this subterranean species varied in the INPA-WWF reserves and in the Reserve Ducke. In areas of high density, S. **salseri** appear to chorus but they also call singly and they only called during rainfall. The advertisement call is a clearly pulsed, short, relatively pure tone having an emphasized frequency of about 1.13 kHz (Table 1; Fig.22). Harmonic frequency bands appear on all sonograms and were also noted by Pyburn (1975). Advertisement calls made by the same individual were very consistent but the call duration and pulse rate varied slightly between individuals (Table 1).

DISCUSSION

The eighteen species of anuran amphibians which were analysed are acoustically dissimilar. The call parameters provided in Tables 1 and 2 may be used to help ascertain the presence and abundance of these species in the cental Amazon. In addition to characterizing the call for each species, certain call parameters may provide information of taxonomic or ecological importance.

The time parameters of most forest frog species differ from open habitat species. Several species of forest frogs characteristically demonstrated one or more of the following temporal parameters: very low call rates; sporadic intervals of calling ; calls were only made on very few nights of the study period (Table 2). The reduced calling time of most forest species is in striking contrast to the virtually continuous calling at high (more than one call per min) rates over several months by almost all of 23 open habitat species in the Manaus area (Hödl, 1977; Zimmerman, 1982).

Also, the density of calling anurans is much lower in the forest than it is in open habitats. In the INPA-WWF reserves, small aggregations of calling individuals (choruses) were rarely encountered even though breeding habitat such as swamps, streams, and pools were visited regularly. In contrast, during the wet season, calling frogs are more often heard in the city of Manaus than in the forest and 15 species of floating meadow frogs produce constant cacophony every night on the banks of the Rio Solimoes and Rio Negro. During some 80 "collecting days" at different localities in the western Amazon of Brazil, Heyer (1976) also found that open habitat species were relatively easy to sample and formed large choruses. Heyer's forest collecting produced few specimens but there was a greater diversity. Heyer observed that many forest ponds did not have breeding frogs even though the ponds seemed to be ideal for anuran reproduction. In those few forest ponds where species were vocalizing and breeding , the species are rare in museum collections.

Adenomera andreae and **Eleutherodactylus fenestratus** are exceptions to these generalizations. These species chorus every dawn and dusk throughout the forest and they also call, even during the day, when there are periods of rain. These species exhibit synchronized chorusing which is another rather distinctive acoustic feature of forest frogs. Dubois (1976) and Schluter (1980) also observed synchronized chorusing among individuals of forest species but little attention has been directed to the functional significance of this type of vocalization. In a synchronized chorus, an individual's call is temporally very close to or even overlaps the call of a neighbouring conspecific male. It is difficult to locate individuals in such a chorus as the sound is rather confusing to the human ear. If other predators experience similar acoustic interference, there could be a distinct advantage for an individual male to engage in synchronized chorusing. The predator avoidance must, of course, be weighed against any confusion which may be experienced by the females. Perhaps this phenomenon is an acoustic example of the "selfish herd" effect proposed by Hamilton (1971). This theory proposes that selfish avoidance of marginal predators would lead to gregarious tendencies in prey species because a single individual obtains cover close to other individuals. Thus, if a frog places its call as close as possible to those of its neighbours , its chances of being singled out by an acoustically orienting predator are reduced compared to individuals which have temporally spaced calls. The effects are analogous to herding or schooling behaviour in other prey species which are threatened by visually orienting predators. Predation may also be a factor which favours reduced call rates and sporadic calling by individuals of other forest anurans which do not have synchronized choruses. It has been clearly shown that such acoustically orienting predators of anuran species do exist in tropical regions (Tuttle and Ryan, 1981; Ryan **et al.**, 1982).

Undoubtedly, the primary function of vocalization by anurans is for species recognition so that females are able to track conspecific males (Greer & Wells, 1981 and many previous studies). Therefore, it is important for a signal to be stereotyped and not ambiguous to the female. Many species, however, are now known to produce complex calls which contain differing numbers and/or kinds of notes (Wells, 1977b). Most studies which investigate complex calling have been associated with male-male competition for mates and territory (Narins & Capranica, 1976; Wells, 1977a; Greer & Wells , 1980; Rand & Ryan, 1981). It is only fairly recently that observations have been made to suggest that the degree of complexity of calling influences the predation risk incurred by individual calling males such as in **Physalaemus pustulosus** (Ryan **et al.**, 1982).

Some species use a compound advertisement call which is composed of two or more distinctly different notes. In the case of the "Co-Qui" call of Puerto Rican **Eleutherodactylus coqui**, the mate attraction ("Co") and male repelling ("Qui") messages are both contained in the two-note call (Narins & Capranica, 1976). The Central Amazon forest species of **Phyllomedusa** (**P. bicolor**, **P. tomopterna**, and **P. vaillanti**) emit compound calls but it is not known if the different notes convey separate messages. Territorial calls, which are distinctive from the advertisement call, are recognized to occur in some anuran species. Littlejohn (1977), speculated that territorial vocalizations coud have reduced specificity and broad frequency band width which might repel all potential competitors from a territory. Territorial calls need only be short range calls which would conserve energy and decrease locatability for distant predators. Although many species in the present study did have one or more distinctive calls in addition to the advertisement call, information was only available for two species (**Phyllomedusa tarsius** and **Eleutherodactylus fenestratus**) which suggested that a territorial function may exist. Additional observations and play-back experimentation with the tape recorder will be required to investigate the function of non-advertisement calls present in the vocabularies of other species. Both **P. tarsius** and **E. fenestratus** had territorial calls which were not as structured as the advertisement call but the intensity of the territorial calls seemed to be equal to that of the advertisement call and males emitting territorial calls were more easily located as these calls were repeated more frequently.

More detailed information and the precise characterization of the modulation process (either AM or FM) can be obtained with the oscilloscope (Marler, 1969). The sonograph, used in the present study, provides a first approximation of a call in time-frequency coordinates with good precision of frequency information (Greenwalt , 1968). Oscilloscope analyses were not considered in the present study because sample sizes were often not large enough to warrant detailed intraspecific or intrageneric comparisons and only a general description of the acoustic community was desired. It is evident, from the information which was obtained, that there exist a number of fundamental problems which require additional study. There must be some factors which limit the numbers of forest species in areas where there appears to be abundant breeding habitat. If low call rates, sporadic calling activity, or synchronized chorusing evolved as mechanisms to avoid predation, it should be possible to find and to study acoustically orienting predators. The functions of various calls are basically unknown.

RESUMO

As vocalizações de 18 espécies de anuros da floresta amazônica foram gravadas em 3 locais: O Parque Nacional de Tapajós, perto de Itaituba, a Reserva Ducke, perto de Manaus, e as reservas do INPA-WWF, perto de Manaus. Parâmetros estruturais e temporais e sonografias dessas vocalizações são apresentadas, incluindo vocalizações não descritas previamente de ***Phyllobates femoralis*****,** ***Centrolenella oyampiensis*****,** ***Osteocephalous taurinus*****,** ***Osteocephalous*** *sp.,* ***Phrynohyas resinifictrix*****,** ***Phyllomedusa bicolor*****;** ***P. tarsius*****,** ***P. tomopterna*****,** ***Eleutherodactylus fenestratus*** *e* ***Synapturanus salseri****. Ao contrário das espécies de habitat aberto, várias espécies de anuros florestais caracteristi-*

camente demonstram um ou mais dos seguintes parâmetros temporais; baixa taxa de vocalizações, intervalos esporadicos de vocalizações, noites infrequentes de vocalizações e côros sincronizados. Também, a densidade de vocalizações de anuros é muito mais baixa na floresta do que no habitat aberto. Hipotetizamos que a predação tem influenciado a evolução do comportamento vocal nos anuros amazônicos. Côros de vocalizações sincronizadas entre indivíduos de espécies florestais acredita-se que seja uma forma acústica da hipótese da " manada egoística " de Hamilton. Desta maneira, se um anuro vocalizasse o mais perto possível dos seus vizinhos, suas chances de ser escolhido por um predador que se orienta acusticamente tendem a ser reduzidas em comparação com indivíduos que vocalizam isoladamente. **Phyllomedusa bicolor** e P. **tomopterna** usam vocalizações compostas. É desconhecida a função de cada nota nessas vocalizações de notas duplas. Foram gravadas vocalizações complexas de **Hyla geographica**, **Eleutherodactylus fenestratus**, e **Phrynohyas resinifictrix**. Até hoje não se sabe qual é a função dessa vocalização não estereotipada.

Table 1. Call Parameters of Anuran Amphibian Species Recorded in the Central Amazon.

Species (number recorded) Call parameter	Number of calls	Mean ± Standard Deviation[1] (Range)
Phyllobates femoralis (1)		
Calls per Minute	11	209.90**
Intercall Interval (sec)	8	0.29 ± 0.03 (0.25 - 0.32)
Call duration (sec)	11	0.52 ± 0.06 (0.34 - 0.56)
1st note: Low frequency range (kHz)	10	2.57 ± 0.11 (2.37 - 2.69)
High frequency range (kHz)	10	2.77 ± 0.11 (2.54 - 2.86)
Note duration (sec)	10	0.03 ± 0.01 (0.02 - 0.05)
2nd note: Low frequency range (kHz)	11	2.44 ± 0.05 (2.38 - 2.53)
High frequency range (kHz)	11	3.05 ± 0.07 (2.91 - 3.16)
Note duration (sec)	11	0.07 ± 0.03 (0.02 - 0.09)
Internote interval (sec)	10	0.09 ± 0.01 (0.08 - 0.12)
FM slope	11	8.10 ± 0.74 (6.62 - 9.22)
Rise time (sec)	11	0.07 ± 0.01 (0.05 - 0.08)
3rd note: Low frequency range (kHz)	11	2.55 ± 0.09 (2.40 - 2.67)
High frequency range (kHz)	11	3.02 ± 0.03 (2.97 - 3.09)
Note duration (sec)	11	0.06 ± 0.02 (0.02 - 0.07)
Internote interval (sec)	11	0.11 ± 0.02 (0.08 - 0.13)
FM slope	11	7.39 ± 0.98 (5.89 - 9.04)
Rise time (sec)	11	0.06 ± 0.01 (0.05 - 0.07)

Table 1. (continued)

Species (number recorded) Call parameter	Number of calls	Mean ± Stardard Deviation[1]	(Range)
Phyllobates femoralis (1) (continued)			
4th note: Low frequency range (kHz)	11	2.47 ± 0.05	(2.38 - 2.56)
High frequency range (kHz)	11	3.07 ± 0.05	(3.02 - 3.13)
Note duration (sec)	11	0.07 ± 0.00	(0.07 - 0.08)
Internote interval (sec)	11	0.08 ± 0.01	(0.07 - 0.09)
FM slope	11	8.28 ± 0.86	(7.32 - 9.55)
Rise time (sec)	11	0.07 ± 0.01	(0.06 - 0.08)
Centrolenella oyampiensis (3 to 8 in chorus)			
Emphasized frequency (kHz)	3	4.84 ± 0.28*	(4.64 - 5.16)
Low frequency range (kHz)	2	3.94*	(3.74 , 4.13)
High frequency range (kHz)	2	5.24*	(5.14 , 5.34)
Calls per minute	3	2.18 ± 1.01*	(1.34 - 3.30)
Call duration (sec)	2	0.13*	(0.10 , 0.15)
Intercall interval (sec)	3	31.44 ±13.23*	(18.16 -44.61)
Hyla boans (2) (1 individual and a chorus)			
Emphasized frequency (kHz)	26	0.71*	(0.44 , 0.98)
Low frequency range (kHz)	26	0.33*	(0.30 , 0.35)
High frequency range (kHz)	26	1.60*	(1.46 , 1.73)
Calls per minute	26	97.13*	(88.18,106.07)
Call duration (sec)	26	0.22*	(0.24 , 0.19)
Intercall interval (sec)	26	0.63*	(0.57 , 0.68)

Table 1 (continued)

Species (number recorded) Call parameter	Number of calls	Mean ± Standard Deviation [1]	(Range)
Hyla geographical Call Type A (4)			
Emphasized frequency (kHz)	59	0.72 ± 0.05*	(0.67 - 0.79)
Low frequency range (kHz)	59	0.44 ± 0.05*	(0.39 - 0.47)
High frequency range (kHz)	59	1.23 ± 0.26*	(0.87 - 1.44)
Call duration (sec)	59	0.27 ± 0.07*	(0.20 - 0.34)
Intercall interval (sec)	59	0.15 ± 0.01*	(0.14 - 0.16)
Pulse rate (pulses/sec)	59	142.95 ±39.91*	(88.95-183.44)
Hyla geographical Call Type B (2)			
Low frequency range (kHz)	69	0.42*	(0.38 , 0.45)
High frequency range (kHz)	69	1.11*	(0.96 , 1.26)
Note duration (sec)	69	0.05*	(0.04 , 0.06)
Internote duration (sec)	69	0.14*	(0.13 , 0.14)
Hyla granosa (4)			
Calls per minute	56	15.05 ±12.58*	(2.02 -29.56)
Emphasized frequency (kHz)	56	1.42 ± 0.10*	(1.26 - 1.53)
Low frequency range (kHz)	56	1.27 ± 0.13*	(1.07 - 1.39)
High frequency range (kHz)	56	1.60 ± 0.05*	(1.53 - 1.64)
Harmonic frequency band (kHz)	56	2.82 ± 0.19*	(2.53 - 3.02)
Call duration (sec)	56	0.18 ± 0.05*	(0.12 - 0.23)
Intercall interval (sec)	56	9.74 ±11.45*	(2.03 -29.66)
Hyla marmorata (2)			
Calls per minute	11	9.61**	
Low frequency range (kHz)	11	1.53**	(1.29 , 1.78)
High frequency range (kHz)	11	3.43*	(3.36 , 3.49)

Table 1. (continued)

Species (number recorded) Call parameter	Number of calls	Mean ± Standard Deviation [1]	(Range)
Hyla marmorata (continued)			
Call duration (sec)	11	0.22*	(0.17 , 0.26)
Puse rate (pulses/ sec)	11	166.62*	(138.94,194.29)
Intercall interval	91	6.25 ± 6.51	(1.12 -48.68)
Osteocephalus taurinus Call Type A (2)			
Emphasized frequency range (kHz)	16.	0.76 to 1.04*	(0.69,0.82)(0.94,1.14)
Low frequency range (kHz)	16	0.49*	(0.47 , 0.50)
High frequency range (kHz)	16	1.49*	(1.34 , 1.63)
Call duration (sec)	16	1.29*	(1.28 , 1.30)
Pulse rate (pulses/sec)	16	39.46*	(36.61 ,42.30)
O. **taurinus** - Small bursts - B (2)			
Low frequency range (kHz)	43	0.40*	(0.35 , 0.46)
High frequency range (kHz)	43	0.92*	(0.82 , 1.01)
Note duration (sec)	43	0.05*	(0.05 , 0.05)
Internote duration (sec)	43	0.20*	(0.19 , 0.20)
FM slope(1)	8	13.86*	
Rise time (sec)(1)	8	0.04*	
O. **taurinus** - Large bursts -B (1)			
Emphasized frequency range (kHz)	17	0.55 to 0.94	(0.46-0.69)(0.85-1.07)
Low frequency range (kHz)	17	0.00 (baseline)	
High frequency range (kHz)	5	1.85 ± 0.17	(1.62 - 2.01)
Note duration (sec)	5	0.15 ± 0.01	(0.13 - 0.16)
Internote duration (sec)	4	0.13 ± 0.03	(0.10 - 0.16)

Table 1. (continued)

Species (number recorded) Call parameter	Number of calls	Mean ± Stardard Deviation[1]	(Range)
Osteocephalus sp. (10)			
Emphasized frequency (kHz)	60	1.62 ± 0.65*	(1.01 - 2.56)
Low frequency range (kHz)	60	0.89 ± 0.33*	(0.30 - 1.59)
High frequency range (kHz)	60	2.84 ± 0.42*	(2.45 - 3.89)
Call duration (sec)	60	0.24 ± 0.07*	(0.15 - 0.36)
Pulse rate (pulses/sec)(6)	6	172.91 ±31.66	(153.81-216.76)
Phrynohyas resinifictrix (9)			
Emphasized frequency (kHz)	13	1.03 ± 0.46*	(0.31 - 1.64)
Call duration (sec)	98	0.49 ± 0.08*	(0.35 - 0.63)
Low frequency range (kHz)	9	0.37 ± 0.07*	(0.23 - 0.46)
High frequency range (kHz)	9	1.85 ± 0.25*	(1.42 - 2.20)
Pulse rate (pulses /sec)	9	183.43 ±16.14*	(159.69-208.56)
Phyllomedusa bicolor - Call Type A(5)			
Emphasized frequency (kHz)	20	0.99 ± 0.08*	(0.92 - 1.09)
Low frequency range (kHz)	20	0.63 ± 0.03*	(0.62 - 0.69)
High frequency range (kHz)	20	1.47 ± 0.14*	(1.34 - 1.65)
Call duration (sec)			
Pulse rate (pulses/sec)(3)	3	131.53 ±19.11*	(112.52-150.74)
Intercall interval (sec)	20	highly variable	
P. bicolor - Call Type B (1)			
Emphasized frequency (kHz)	10	0.64 ± 0.04	(0.58 - 0.72)
Low frequency range (kHz)	10	0.61 ± 0.05	(0.57 - 0.67)
High frequency range (kHz)	10	1.05 ± 0.20	(0.65 - 1.07)

Table 1. (continued)

Species (number recorded) Call parameter	Number of calls	Mean ± Standard Deviation[1]	(Range)
P. bicolor - Call Type B(1)(cont.)			
Note duration (sec)	10	0.04 ± 0.01	(0.03 - 0.06)
Internote duration (sec)	10	0.07 ± 0.01	(0.06 - 0.07)
Phyllomedusa tarsius - Call Type A			
First Note (3)			
Emphasized frequency (kHz)	23	0.87 ± 0.34*	(0.57 - 1.42)
Low frequency range (kHz)	23	0.41 ± 0.05*	(0.35 - 0.44)
High frequency range (kHz)	23	1.07 ± 0.13*	(0.95 - 1-21)
Note duration (sec)	23	0.06 ± 0.01*	(0.06 - 0.07)
Pulse Rate (pulses/ sec)	23	99.54 ±11.13*	(86.98-108.19)
Call rate (Calls/min)	23	1.43 ± 0.06*	(0.61 - 2.69)
Intercall interval (sec)	23	52.23 ±28.02*	(22.32 -98.57)
Second note (2)			
Low frequency range (kHz)	14	0.35 ± 0.04	(0.29 - 0.44)
High frequency range (kHz)	14	1.13 ± 0.13	(0.98 - 1.32)
Note duration (sec)	14	0.03 ± 0.01	(0.02 - 0.06)
Pulses per note	14	2.50 ± 0.50	(2.00 - 3.00)
Internote duration (sec)	14	0.12 ± 0.03	(0.07 - 0.14)
P. tarsius - Call Type B (2)			
Emphasized frequency (kHz)	36	0.54*	(0.12 , 0.85)
Low frequency range (kHz)	36	0.42*	(0.39 , 0.45)
High frequency range (kHz)	36	1.46*	(1.28 , 1.64)
Note duration (sec)	36	0.06*	(0.06 , 0.06)
Internote duration (sec)	36	0.08*	(0.09 , 0.06)
Internote series interval (sec)	36	8.36*	(12.94 , 3.77)

Table 1. (continued)

Species (number recorded) call parameter	Number of calls	Mean ± Standard Deviation [1]	(Range)
Phyllomedusa tomopterna - "Chuck" Call Type (2 small choruses)			
Low frequency range (kHz)	19	1.32*	(1.18 , 1.45)
High frequency range (kHz)	19	2.25*	(2.20 , 2.30)
Note duration (sec)	19	0.12*	(0.11 , 0.13)
Pulse rate (pulses/ sec)	19	204.55**	
Call rate (Calls/ min)	19	much less than 1**	
P. tomopterna - "Whirr" Call Type (1)			
Low frequency range (kHz)	5	0.83 ± 0.03	(0.79 - 0.85)
High frequency range (kHz)	5	1.40 ± 0.10	(1.29 - 1.50)
Note duration (kHz)	5	0.27 ± 0.05	(0.22 - 0.33)
Pulse rate (pulses/ sec)	5	109.92 ±17.41	(96.90-108.32)
Intercall Type interval(sec)	5	0.48 ± 0.14	(0.40 - 0.76)
Adenomera andrea (5)			
Emphasized frequency range (kHz)	52	4.10 ± 0.18* to 4.43 ± 0.21*	
Ranges of emphasized frequency(kHz)	52	(3.69 - 4.14)*to(4.07 - 461)*	
Low frequency range (kHz)	52	3.76 ± 0.19*	(3.44 - 3.91)
High frequency range (kHz)	52	4.63 ± 0.23*	(4.24 - 4.84)
First harmonic frequency (kHz) (2)	2	2.21*	(2.19 - 2.23)
Call rate (calls/min)	52	79.59 ±43.92*	(48.99-144.65)
Call duration (sec)	52	0.08 ± 0.01*	(0.06 - 0.10)
Intercall interval (sec)	52	(0.96 ± 0.50)*	(0.41 - 1.66)

Table 1.(continued)

Species (number recorded) Call parameter	Number of calls	Mean ± Standard Deviation[1]	(Range)
Eleutherodactylus fenestratus - Advertisement call (4)			
Emphasized frequency 1st note (kHz)	77	2.02 ± 0.48*	(1.65 - 2.06)
Emphasized frequency 2nd note (kHz)	77	3.02 ± 0.15* to 3.52 ± 0.22*	
2nd note ranges (kHz)	77	(2.82 - 3.23)*to(3.20 - 3.76)*	
Low frequency range (kHz)	77	1.52 ± 0.11*	(1.35 - 1.57)
High frequency range (kHz)	77	3.84 ± 0.94*	(2.35 - 4.91)
Internote duration (sec)	77	0.11 ± 0.08	(0.05 - 0.23)
Pulse rate (pulses/sec)	77	259.97 ±20.62	(231.42-279.56)
Call duration (sec)	77	0.12 ± 0.08*	(0.07 - 0.25)
E. **fenestratus** - Repeated burst Territorial call (2)			
Low frequency range (kHz)	30	1.38*	(1.28 , 1-48)
High frequency range (kHz)	30	4.15*	(3.85 , 4.44)
Burst duration (sec)	30	0.04*	(0.04 , 0.04)
Interburst duration (sec)	30	0.03*	(0.03 , 0.03)
E. **fenestratus** - Single burst with FM harmonics Territorial call (1) "playback experiment"			
Emphasized frequency 1st note (kHz)	16	1.74 ± 0.09	(1.64 - 1.91)
Emphasized frequency 2nd note (kHz)	26	2.86 ± 0.14 to 3.35 ± 0.18	
2nd note ranges (kHz)	26	(2.55 - 3.06)to (3.13 - 3.63)	
Low frequency range (kHz)	28	1.48 ± 0.13	(1.11 - 1.66)
High frequency range (kHz)	28	4.38 ± 0.44	(3.47 - 5.03)
Harmonic interval (kHz)	12	0.23 ± 0.01	(0.22 - 0.25)
Note duration (sec)	24	0.05 ± 0.01	(0.03 - 0.01)

Table 1. (continued)

Species (number recorded) Call parameter	Number Of calls	Mean ± Standard Deviation [1] (Range)
Eleutherodactylus fenestratus (cont.)		
Pulse rate (pulses/sec)	4	270.42 ± 33.31 (223.03 - 298.08)
FM slope	37	6.89 ± 2.85 (2.50 - 14.91
Rise time (sec)	37	0.03 ± 0.01 (0.01 - 0.05)
"call station"		
Emphasized frequency 1st note (kHz)	3	0.86 ± 0.09 (0.77 - 0.93)
Emphasized frequency 2nd note (kHz)	3	1.35 ± 0.04 to 2.00 ± 0.18
2nd note ranges (kHz)	3	(0.77 - 0.93) to (1.30 - 1.38)
Low frequency range (kHz)	3	0.66 ± 0.07 (0.60 - 0.73)
High frequency range (kHz)	3	2.53 ± 0.13 (2.45 - 2.70)
Note duration (sec)	3	0.07 ± 0.02 (0.06 - 0.09)
FM slope	3	16.22 ± 1.29 (15.42 - 17.70)
Rise time (sec)	37	0.04 ± 0.01 (0.04 - 0.05)
"fight"		
Emphasized frequency 1st note (kHz)	12	1.67 ± 0.15 to 2.12 ± 0.19
1st note ranges (kHz)	12	(1.45 ± 1.85) to (1.89 - 2.47)
Emphasized frequency 2nd note (kHz)	10	2.94 ± 0.11 (2.71 - 3.08)
Low frequency range (kHz)	14	1.33 ± 0.07 (1.16 - 1.42)
High frequency range (kHz)	14	3.54 ± 0.17 (3.27 - 3.94)
Harmonic interval (kHz)	7	0.19 ± 0.01 (0.18 - 0.21)
Note duration (sec)	14	0.07 ± 0.03 (0.03 - 0.11)
Pulse rate (pulses/sec)	9	204.68 ± 21.58 (167.67 - 221.41)

Table 1. (continued)

Species (number recorded) Call parameter	Number of calls	Mean ± Standard Deviation[1] (Range)
Eleutherodactylus fenestratus (cont.)		
"fight sequence squeal" (2)		
Emphasized frequency 1st note (kHz)	11	1.72 ± 0.10 to 2.23 ± 0.15
1st note ranges (kHz)	11	(1.52 - 1.83) to (2.09 - 2.51)
Emphasized frequency 2nd note (kHz)	4	2.35 ± 0.07 to 3.03 ± 0.11)
2nd note ranges (kHz)	4	(2.29 - 2.43) to (2.97 - 3.12)
Low frequency range (kHz)	11	1.49 ± 0.07 (1.36 - 1.59)
High frequency range (kHz)	11	3.59 ± 0.16 (3.35 - 3.82)
Harmonic interval (kHz)	11	0.19 ± 0.08 (0.17 - 0.42)
Call duration (sec)	11	0.26 ± 0.08 (0.17 - 0.42)
Pulse rate (pulses/sec)	11	201.83 ±11.09 (191.49-203.98)
Leptodactylus amazonicus (1)		
Emphasized frequency (kHz)	8	1.03 ± 0.04 (0.98 - 1.10)
Low frequency range (kHz)	8	0.76 ± 0.04 (0.70 - 0.83)
High frequency range (kHz)	8	1.14 ± 0.02 (1.10 - 1.17)
Call duration (sec)	11	0.19 ± 0.01 (0.16 - 0.20)
Intercall interval (sec)	320	1.18 ± 2.28 (0.22 -22.67)
Pulse rate (pulses/sec)	8	67.98 ± 2.80 (65.40 -72.58)
Call rate (calls/min)	8	50.97**
FM slope	8	0.83 ± 0.16 (0.50 - 1.00)

Table 1. (continued)

Species (number recorded) Call parameter	Number of calls	Mean ± Standard Deviation [1]	(Range)
Leptodactylus pentadactylus (7)			
Emphasized frequency (kHz)	59	0.81 ± 0.07*	(0.77 - 0.92)
Low frequency range (kHz)	59	0.55 ± 0.17*	(0.70 - 0.83)
High frequency range (kHz)	59	0.94 ± 0.06*	(0.88 - 1.02)
Call duration (sec)	59	0.61 ± 0.25*	(0.16 - 0.25)
Intercall interval (sec)	59	6.24 ± 4.99*	(1.37 -11.51)
Call rate (calls/min)	59	20.55 ±15.98*	(4.43 -32.78)
FM slope	59	4.73 ± 1.80*	(1.87 - 6.45)
Rise time (sec)	59	0.14 ± 0.04*	(0.09 - 0.19)
Leptodactylus wagneri (3)			
Emphasized frequency 1st note (kHz)	35	1.05 ± 0.12*	(0.91 - 1.14)
Emphasized frequency 2nd note (kHz)	35	1.95 ± 0.10*	(1.86 - 2.06)
Emphasized frequency 3rd note (kHz)(2)	20	2.37*	(2.29 - 2.44)
Low frequency range (kHz)	35	0.78 ± 0.08*	(0.69 - 0.85)
High frequency range (kHz)	35	2.39 ± 0.09*	(2.30 - 2.48)
Call duration (sec)	35	0.04 ± 0.01*	(0.04 - 0.05)
Intercall interval (sec)	35	0.81 ± 0.29*	(0.61 - 1.14)
Call rate (calls/min)	35	80.45 ±24.37*	(52.84 -98.95)
Synapturanus salseri (3)			
Emphasized frequency (kHz)	34	1.13 ± 0.01*	(1.13 - 1.14)
Low frequency range (kHz)	34	0.99 ± 0.05*	(0.95 - 1.05)
High frequency range (kHz)	34	1.32 ± 0.10*	(1.24 - 1.43)
Frequency of 1st harmonic (kHz)	34	2.22 ± 2.22*	(2.12 - 2.33)

Table 1.(continued)

Species (number recorded) Call parameter	Number of calls	Mean ± Standard Deviation[1]	(Range)
Synapturanus salseri (cont.)			
Call duration (sec)	34	0.30 ± 0.09*	(0.20 - 0.38)
Call rate (calls/ min)	34	6.41 ± 4.85*	(2.96 -11.95)

1 The values which are marked* are the averaged means for the individuals analysed. In such cases, the standard deviation are standard deviations of the averaged mean values and the ranges are ranges of individual mean values. This method of analysis provides an inter- individual comparison.

** all the available calls were used for calculation (calls/time).

Table 2. Calling frequency, diel period, and call rate of frogs in the primary forest of the INPA-WVF reserves between February and mid-july.

Species	Calling Frequency [1]	Diel Period[2]	Mean Advertisement Call Rate [3] Calls/Min (number of individuals)
Phyllobates femoralis	sporadically	D	206.90 (1)
Centrolenella oyampiensis	frequently	N	2.18 (3)
Hyla boans	frequently (after june)	N	97.13 (3)
Hyla geographica	frequently	N	variable (more than 10)
Hyla granosa	sporadically	N	15.05 (6)
Hyla marmorata	rarely	N	9.61 (1)
Osteocephalus taurinus	frequently (Feb. to May)	N	less than .06 (more than 10)
Osteocephalus sp.	every (Feb. to May)	D/N	1.69 to 5 (more than 10)
Phrynohyas resinifictrix	every	N	9.46 (9)
Phyllomedusa bicolor	sporadically	N	less than .72 (10)
Phyllomedusa tarsius	frequently	N	1.43 (4)
Phyllomedusa tomopterna	sporadically	N	variable low (more than 10)
Adnomera andreae	every	D	79.59 (5)
Eleutherodactylus fenestratus	every	D/N	6.28 (3)
Leptodactylus amazonicus	rarely	N	50.97 (1)
Leptodactylus pentadactylus	sporadically	D/N	20.55 (9)
Leptodactylus stenodema	rarely	N	8.70 (1)
Leptodactylus wagneri	rarely	N	80.45 (3)
Synapturanus salseri	sporadically	D/N	6.41 (3)

1. The species were heard: rarely (less than 5 study nights per month); sporadically (5 to 10 study nights/days per month); frequently (10 to 15 study nights/days per month); or every and or day.
2. The diel period was either diurnal (D), nocturnal (N), or both (D/N).
3. Variable calls had wide ranges and large standard deviations (see Table 1) so the means are not representative. The call rate provide is the maximum call rate which was recorded.

FIG. 1. Rainforests of South America (adapted from Lynch, 1979).

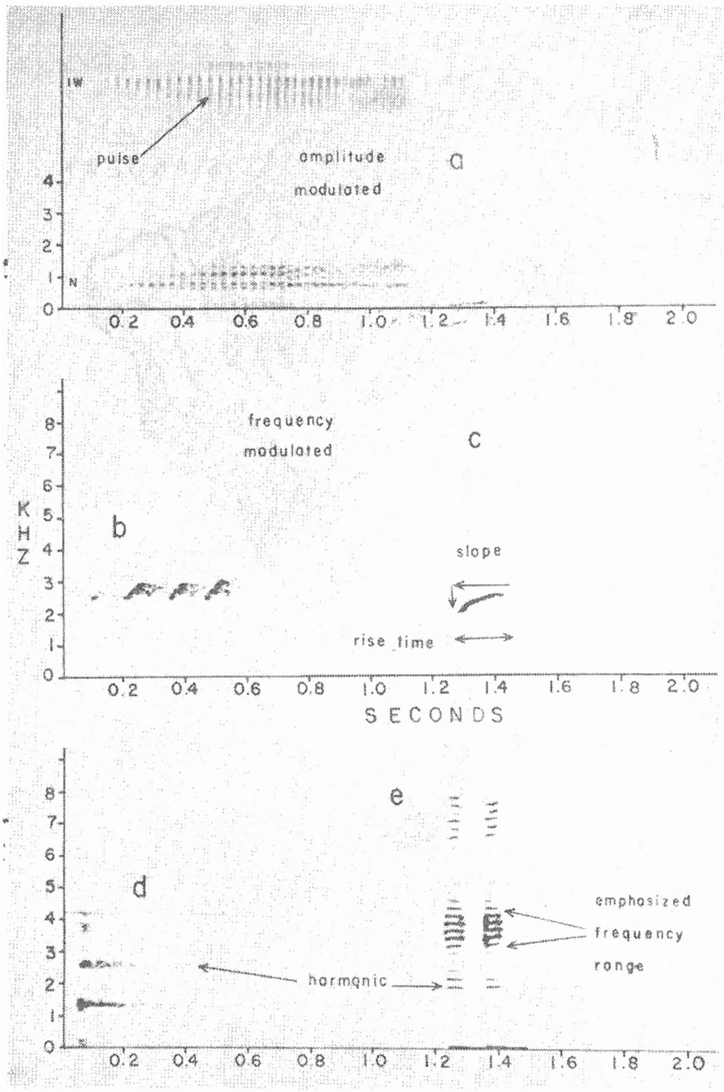


FIG. 2. a - Examples of an amplitude modulated (AM) call with broad frequency range (from **Osteocephalus taurinus**). A single pulse is shown. b, c - Narrow band(N) examples of tonal frequency modulated (FM) calls from Phyllobates (b) and **Leptodactylus pentadactylus** (c). Measurements taken for FM slope and rise time are shown in c. Slope equals rise (vertical arrow) divided by run (horizontal arrow). d - Narrow band example of a tonal call with harmonics (from **Hyla granosa**). e - Narrow band example of a call with broad frequency range, harmonic, and range of emphasized frequency (from **Eleutherodactylus fenestratus**). In all figures, N is a narrow frequency filter band width tracing, W is a wide frequency filterband tracing with an inverted scale, and S is a section of energy through a call.

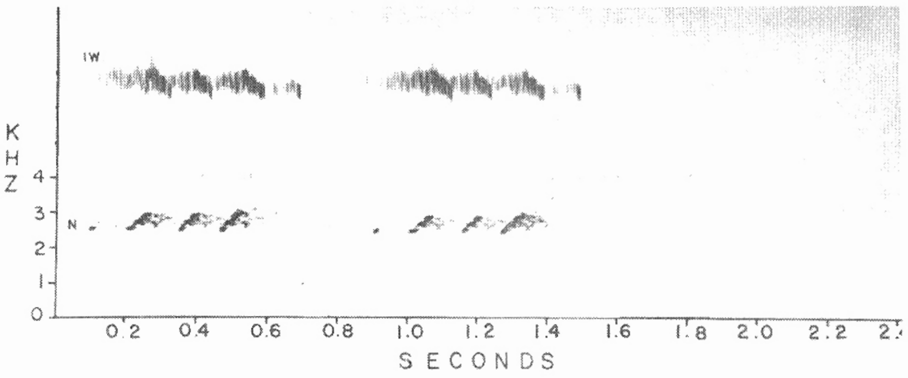


FIG. 3. Two advertisement calls recorded from a **Phyllobates femoralis** in Reserve Ducke.

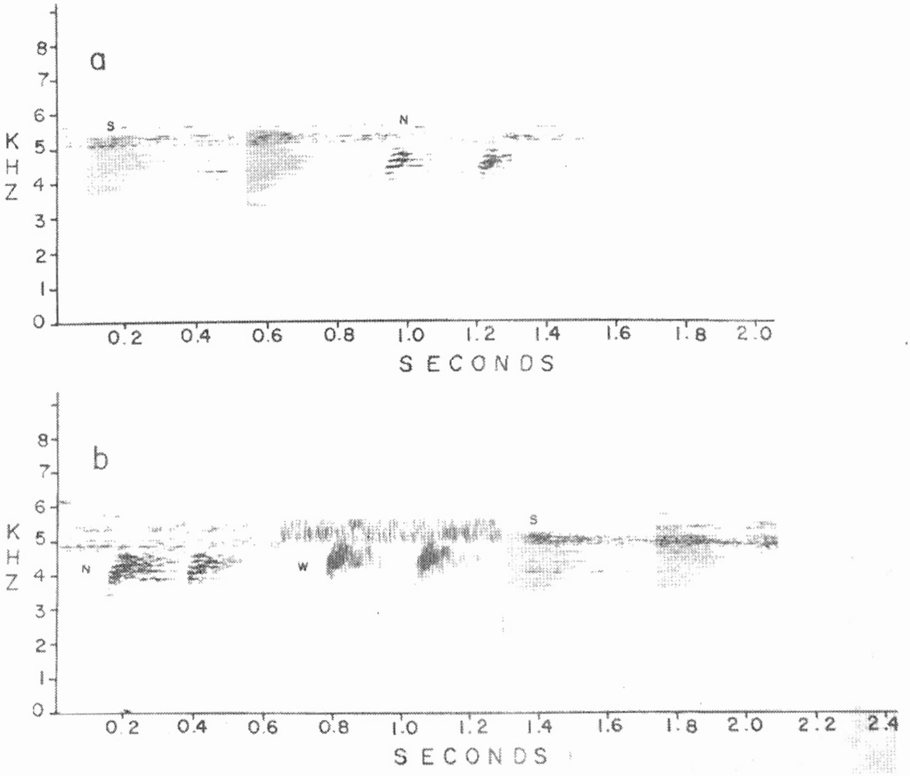


FIG. 4. Advertisement calls of **Centrolenella oyampiensis** recorded from two (a and b) INPA-WWF individuals.

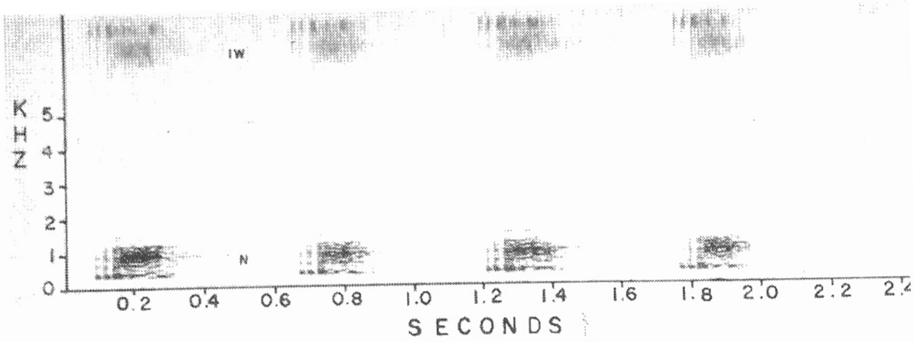
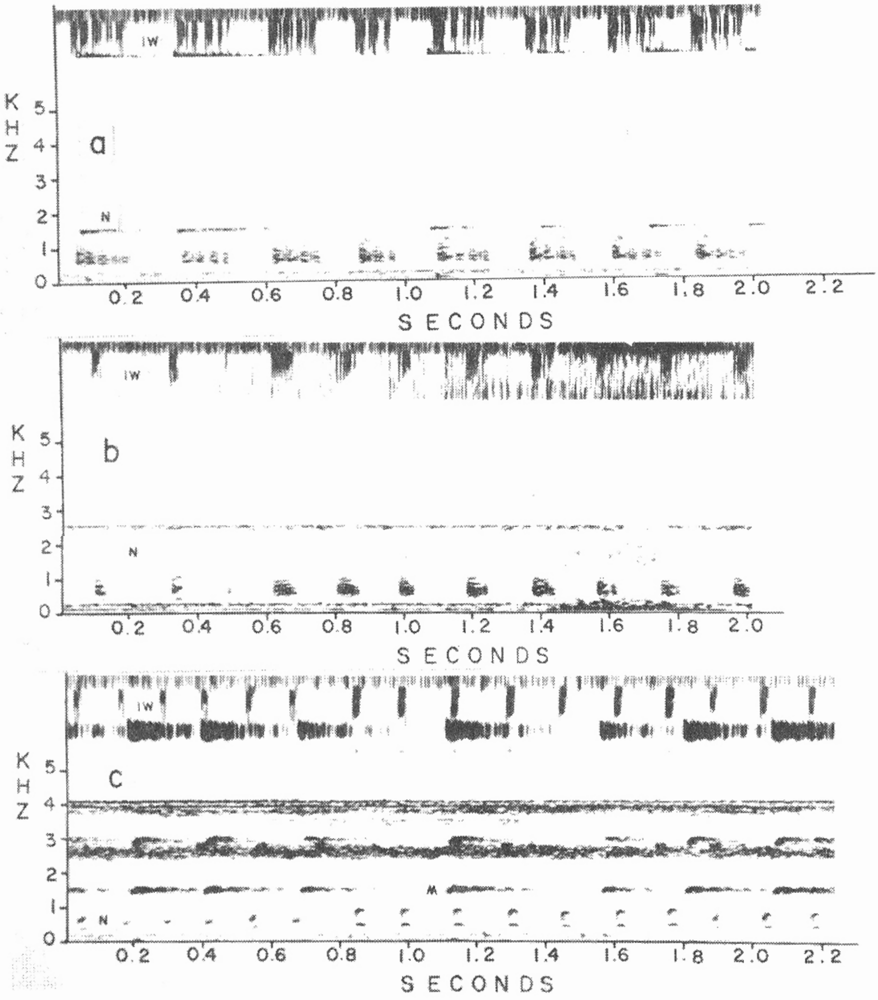


FIG. 5. Four advertisement calls recorded from a INPA-WWF **Hyla boans**.



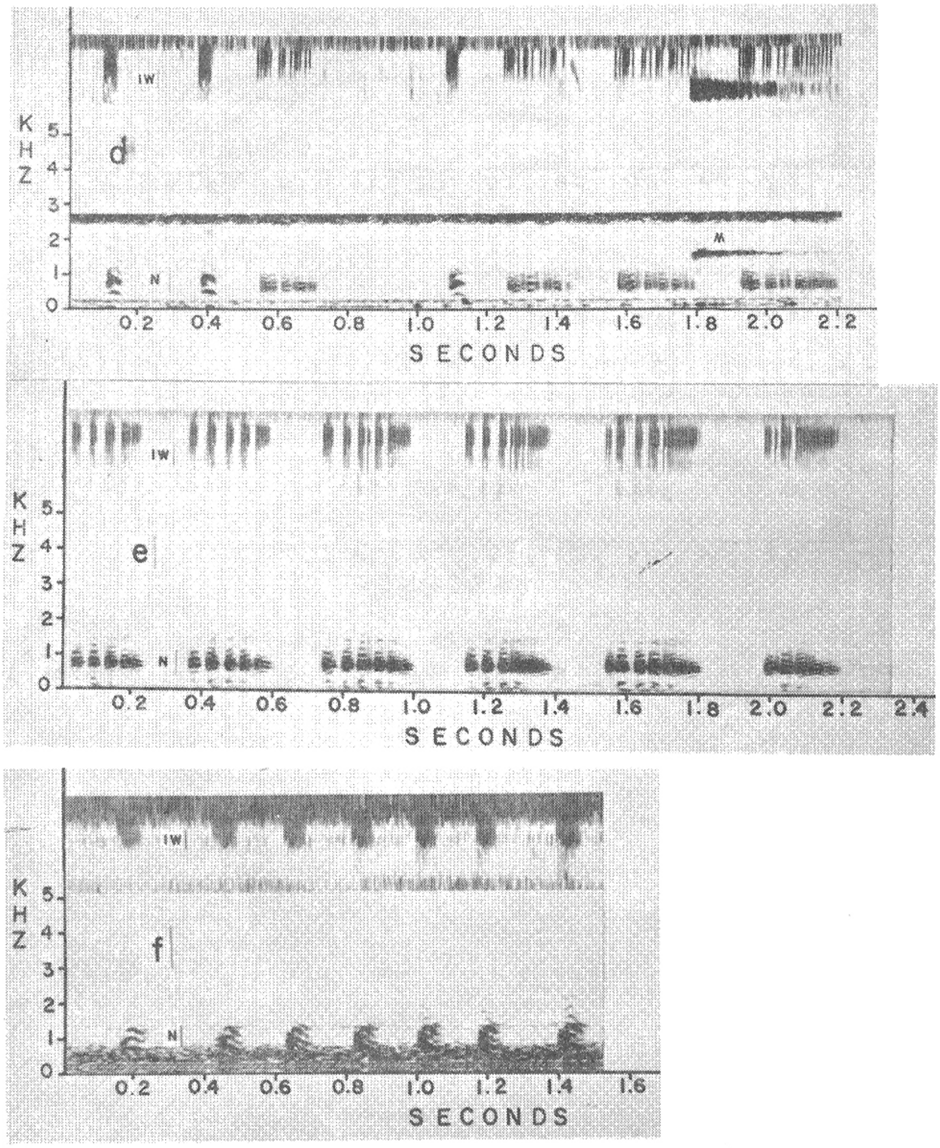


FIG. 6. Vocalizations of **Hyla geographica**. Type A (a) and Type B (b,c) vocalizations were recorded from the same individual. M (in c) is a call of **Hyla granosa**. Type A (d,c) and Type B (d,f) vocalizations were recorded from individuals in the Tapajós National Park.

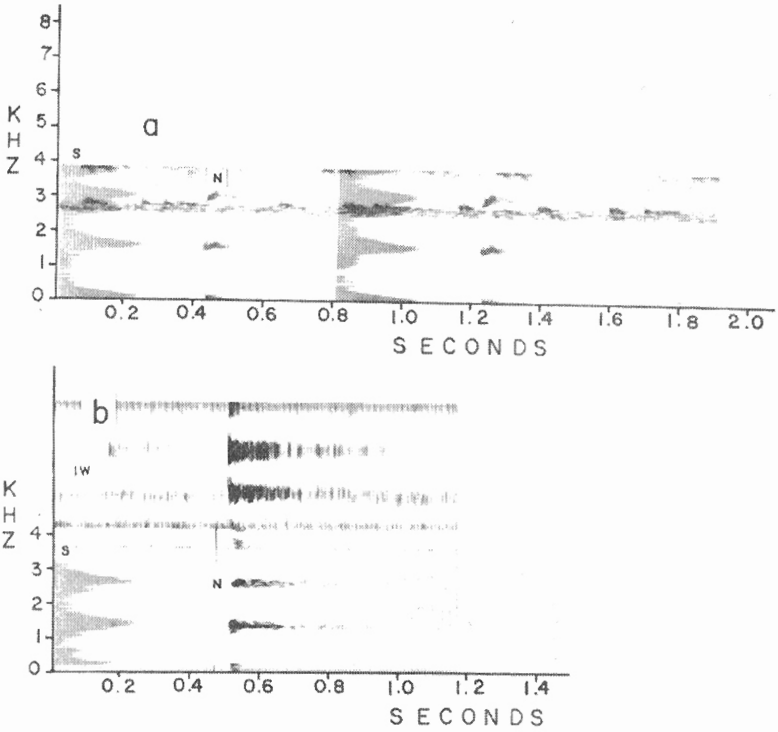


FIG. 7. Advertisement calls of **Hyla granosa** recorded in the INPA-WWF reserves (a) and the Tapajós National Park (b).

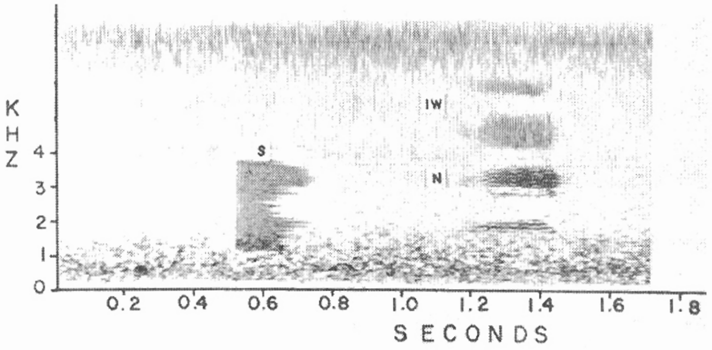


FIG. 8. An advertisement call recorded from a **Hyla marmorata** in the Tapajós National Park. The dark background is the noise produced from rapids on the Tapajós river.

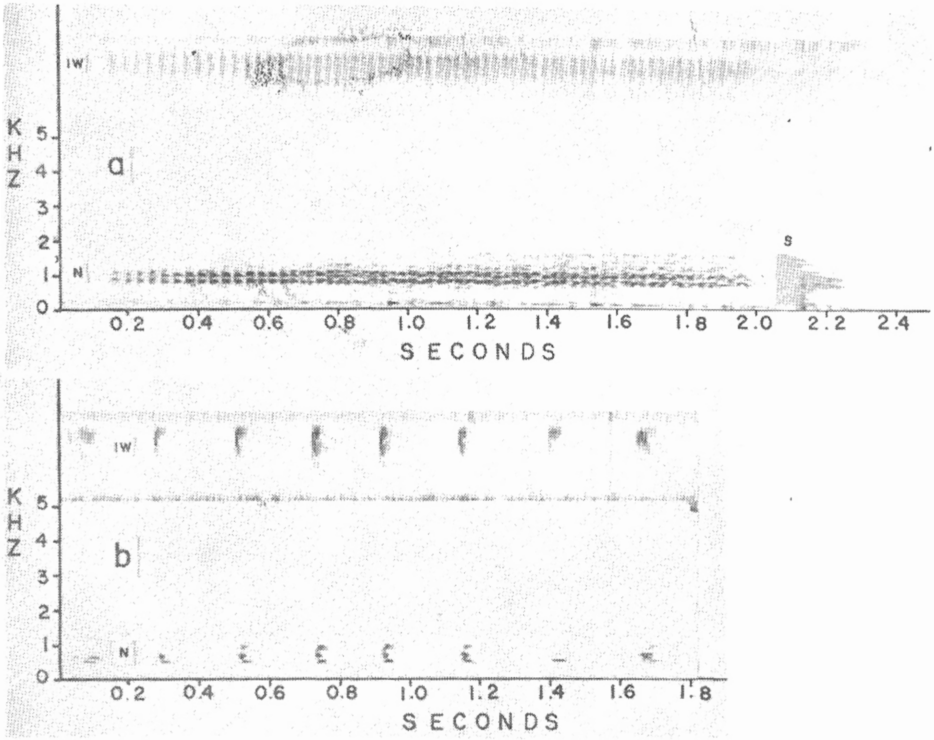


FIG. 9. Vocalizations produced by **Osteocephalus taurinus.** Type A (a) an Type B (b) calls are from a Tapajós National Park. Individual.

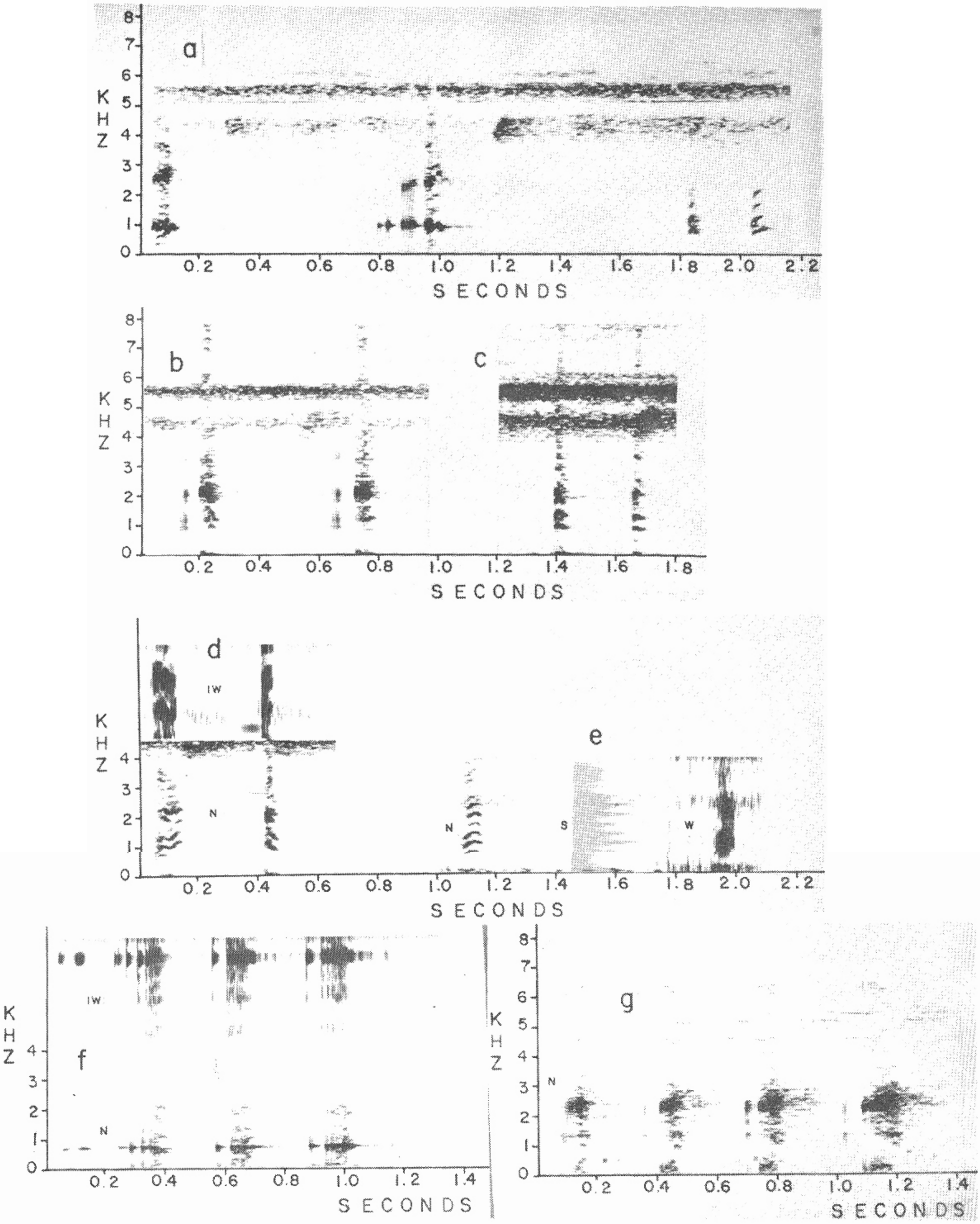


FIG. 10. Vocalizations (a to e, and f) made by an INPA-WWF **Osteocephalus sp.**, and a Tapajós National Park **Osteocephalus sp.** (f). S (in e) is a section of the call to the left.

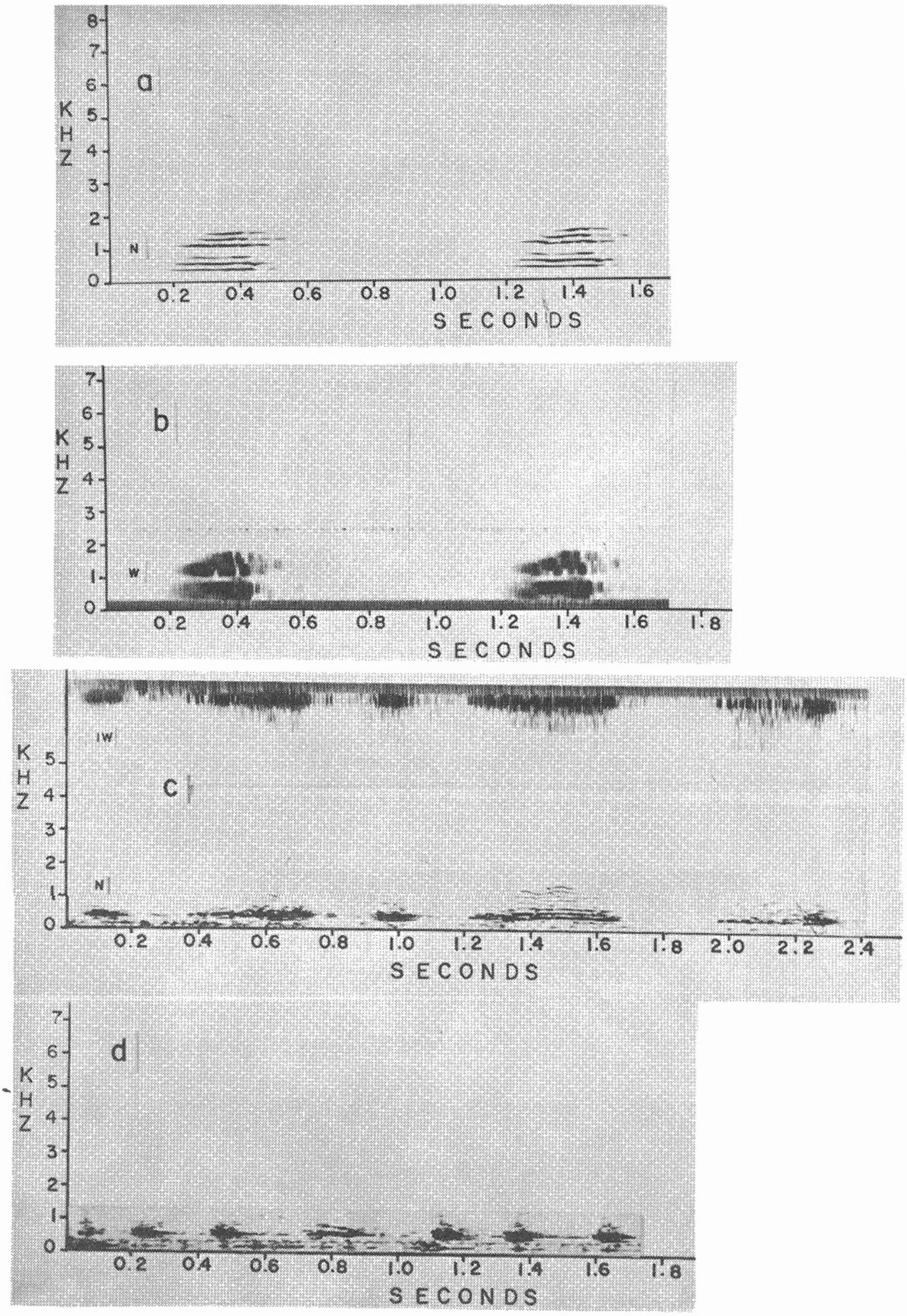


FIG. 11. Vocalizations of two **Phynohyas resinifictrix** individuals recorded in the INPA-WWF reserves. Shown are narrowband tracings of two Type A calls (a); wide band tracings (b) of the calls in a; and Type B vocalization.

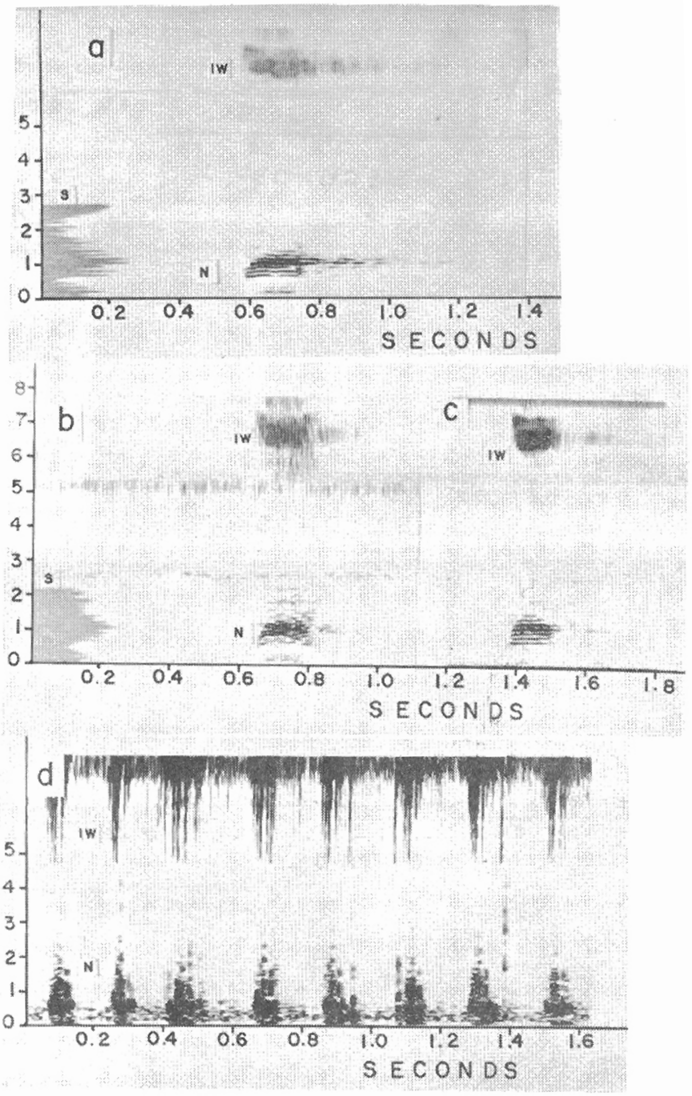


FIG. 12. Advertisement calls of there **Phyllomedusa bicolor** (a,b,c) recorded in the INPA WWF reserves. An agonistic (Type B) vocalization is shown in d. Sections are through calls to the right.

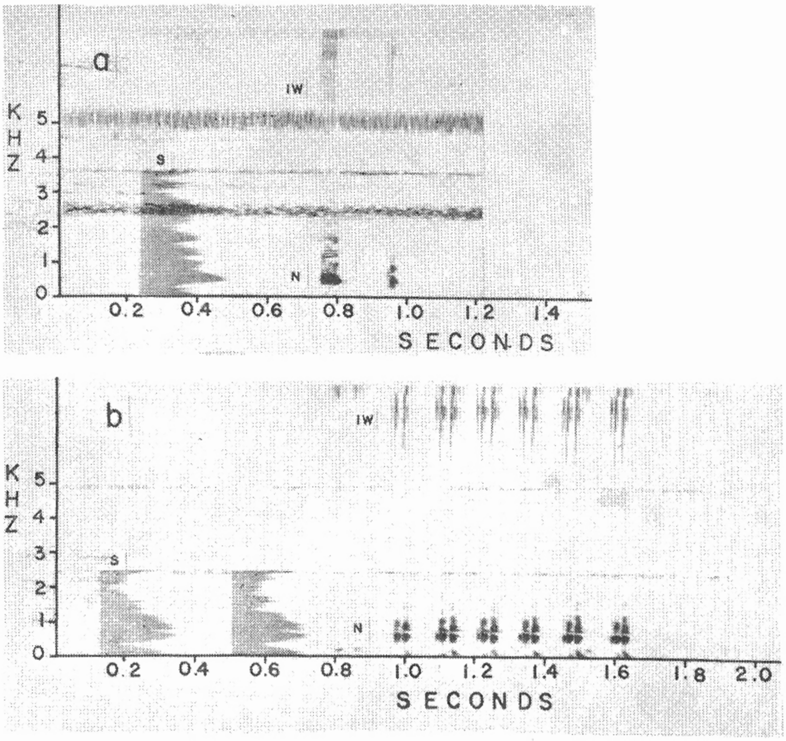


FIG. 13. Advertisement call (a) and territorial vocalization (b) of a **Phyllomedusa tarsius** recorded in the INPA-WWF reserves. S (in a) is section through the first note. In c, the first and second sections are through the first and second notes of the series.

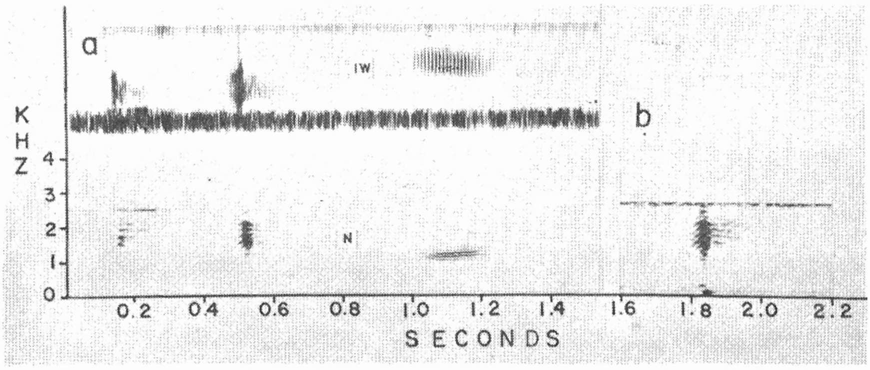
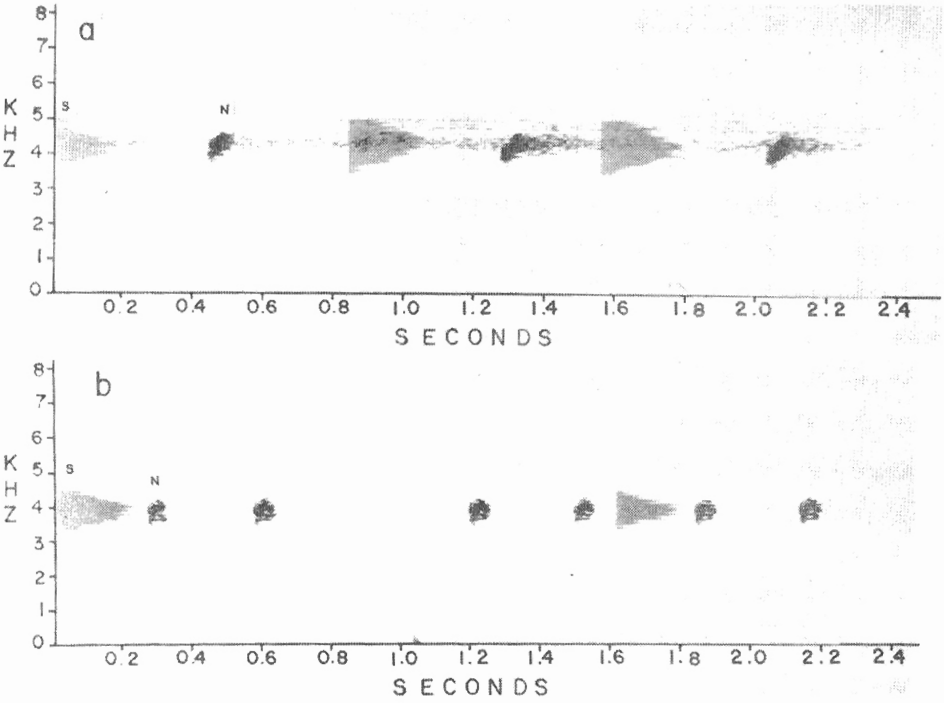


FIG. 14. Vocalizations made by two (a and b) **Phyllomedusa tomopterna** in the Reserve Ducke.



IG. 15. Advertisement calls of **Adenomera andreae** recorded from an INPA-WWF (a) individual and from a Reserve Ducke individual (b).

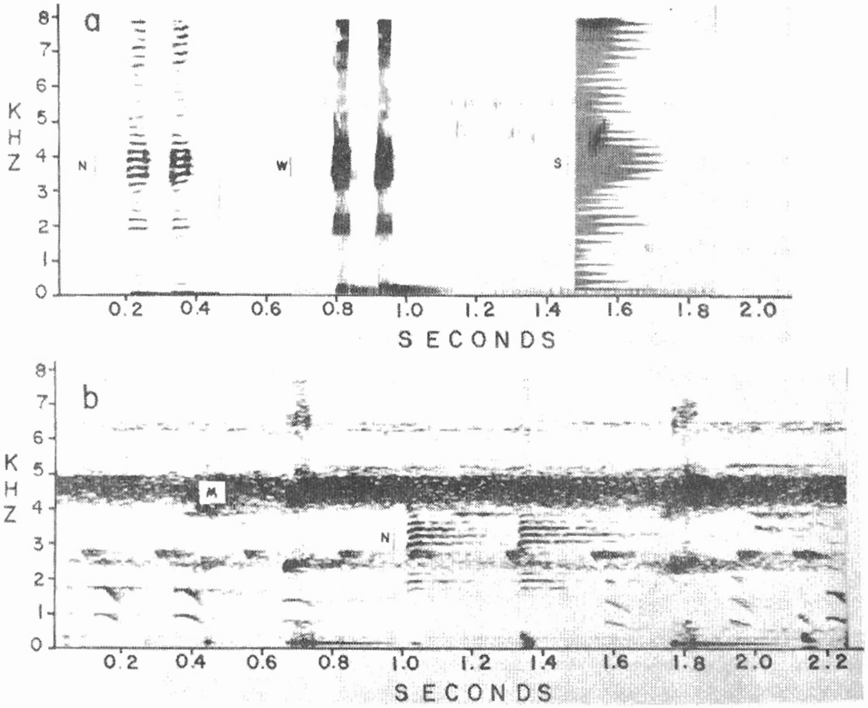


FIG. 16. Advertisement calls of two (a and b) **Eleutherodactylus fenestratus** individuals recirded in the INPA-WWF reserves. M. (in b) is the background noise from calling **Adenomera andreae** and Z is derived from bird vocalizations.

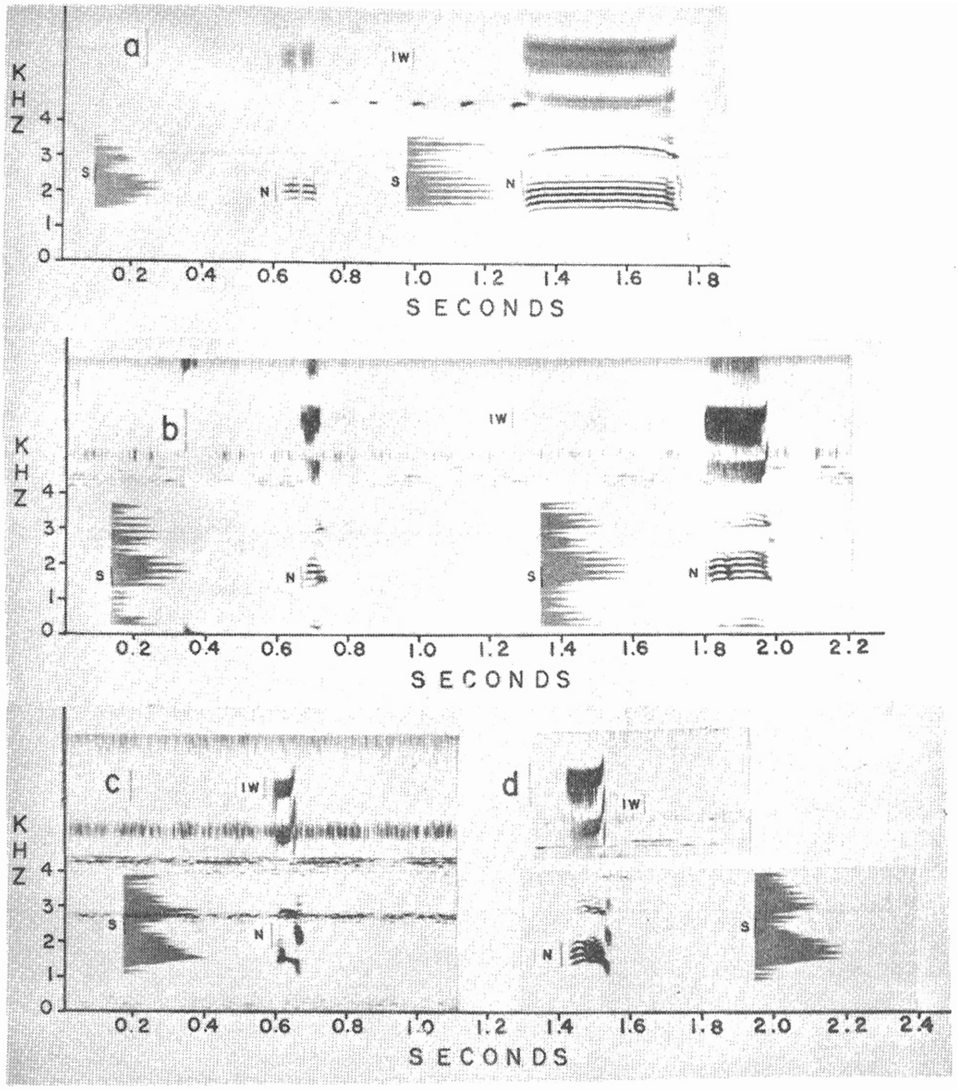


FIG. 17. Narrow band tracings of territorial vocalizations produced by an INPA-WWF **Eleutherodactylus fenestratus** (a,b,c) calling in response to the advertisement calls (M) of a nearby conspecific. **E. fenestratus** territorial calls (d,e,f) were elicited by playback of a conspecific advertisement call. The section is through the call to the left.

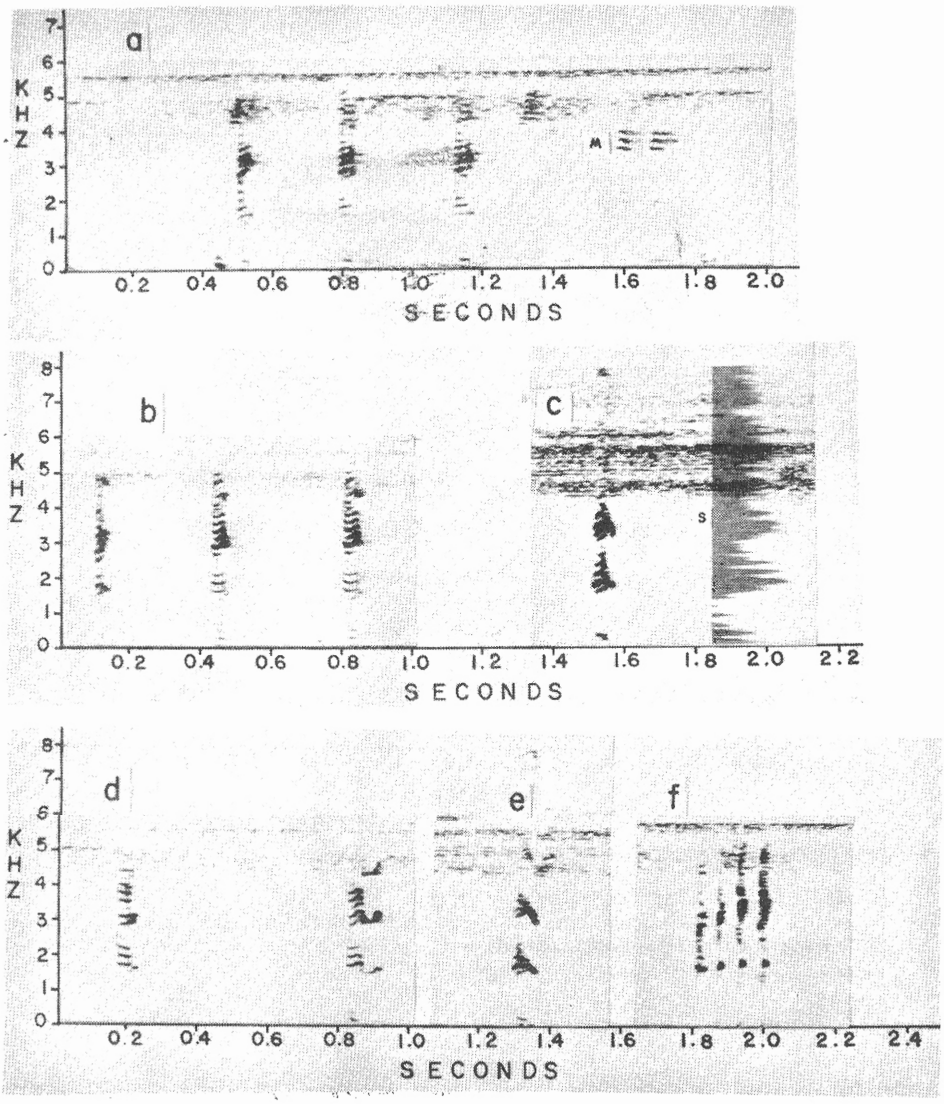


FIG. 18. Vocalizations made by two **Eleutherodactylus fenestratus** individuals emitted while fighting in the Tapajos National Park. They produced "squeal"calls (a) and "short burst" vocalizations (b,c,d). Sections (in a, b and c)are through calls to the right. The section in d is through the call to the left.

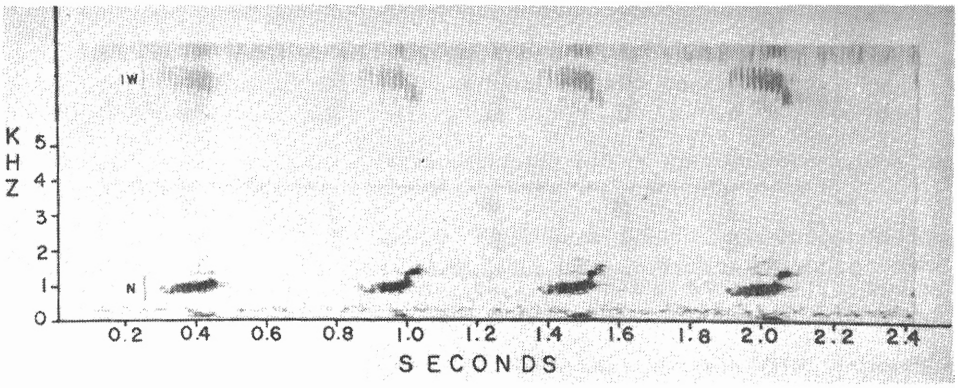


FIG. 19. Advertisement calls of an INPA-WWF **Leptodactylus amazonicus**.

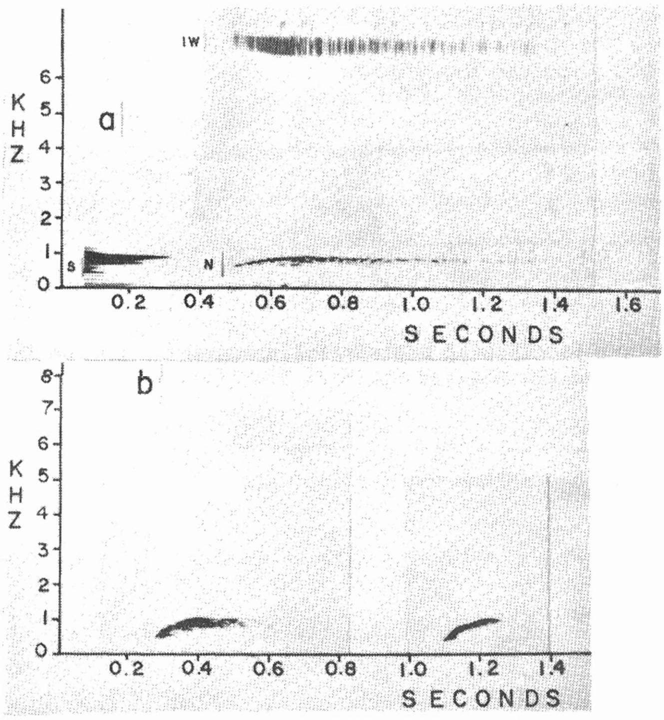


FIG. 20. Advertisement calls of three **Leptodactylus pentadactylus** from INPA-WWF reserves (a) and the Reserve Ducke (b).

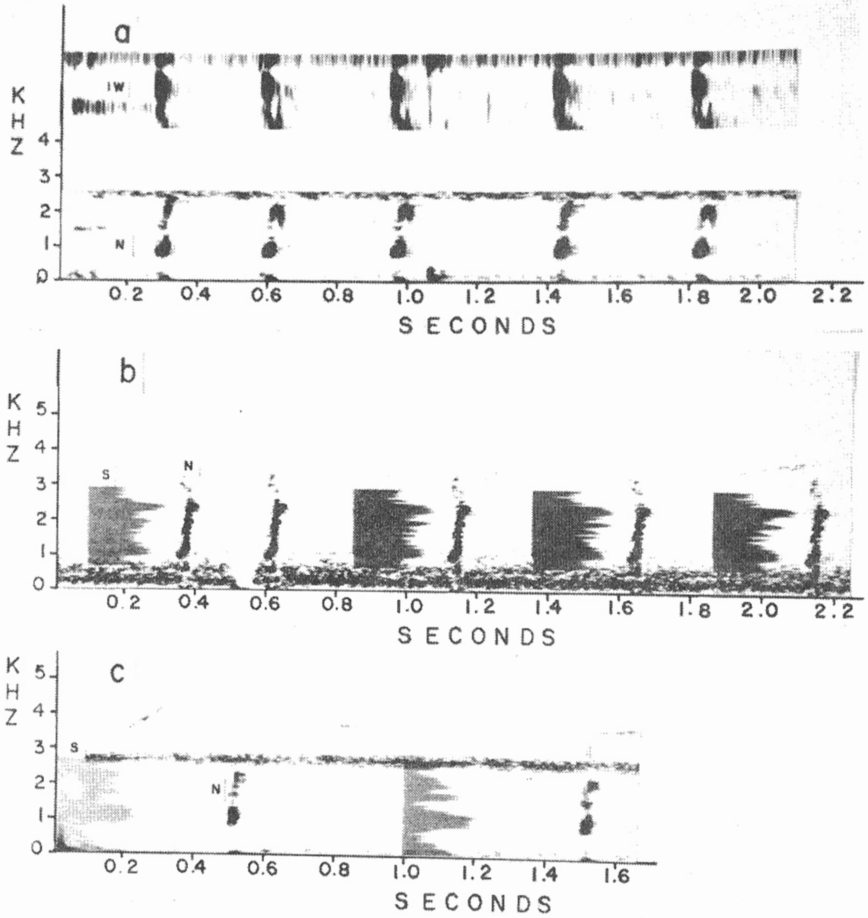


FIG. 21. Advertisement calls of three **Leptodactylus wagneri** recorded in the INPA - WWF reserves (a,c) and the Tapajos National Park (b).

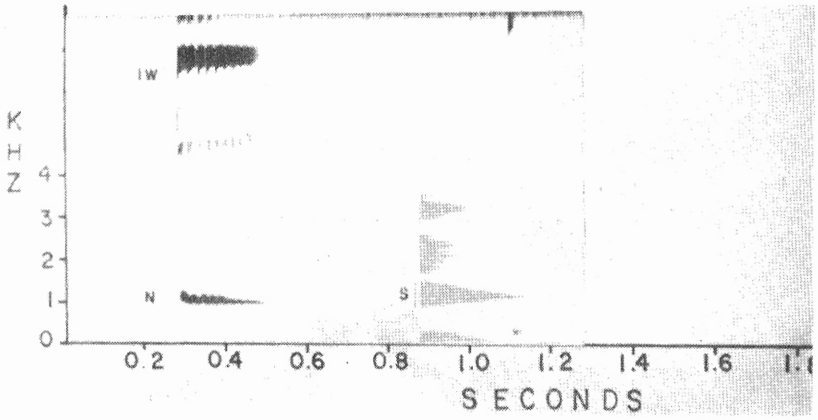


FIG. 22. Advertisement call of an INPA-WWF **Synapturanus salseri**.

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