THE ADVERTISEMENT CALLS OF TWO ENDANGERED SPECIES OF ENDEMIC PHILIPPINE FROGS: *Platymantis spelaeus* and *P. insulatus* (Anura; Ranidae)

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ABSTRACT

We provide the first published accounts of the acoustic mate-recognition signals of the Negros cave frog, Platymantis spelaeus, and the Gigante Island frog, P. insulatus. Both species are endemic to the Visayan Pleistocene Aggregate Island Complex (and are from Negros and Gigante islands, respectively), and both species are considered to be at some level of vulnerability of extinction due to the activities of humans in their very restricted geographical ranges.

On the limestone outcrops of the Municipality of Basay in southern Negros Island, P. spelaeus calls in and around caves and crevices of porous limestone karst. The mating calls of males of the species are unusually complex, consisting of paired calls of two separate syllables (=notes) each. Each note is a tonal frequency arc, and one portion of the second note is vibrational and amplitude modulated. In paired calls, the first note of the second call possesses relatively rich harmonic structure (up to five distinct harmonics of the fundamental frequency); remaining notes may have up to three harmonics.

The Gigante Island group endemic P. insulatus still persists despite near complete removal of original vegetation on the islands in this small land-bridge archipelago. Platymantis insulatus calls from crevices and small cave openings in limestone cliffs and outcrops following heavy rains. The mating call of this species is pulsed and highly amplitude-modulated, consisting of a long pulse train, with a gradually increasing pulse rate and decreasing interpulse interval throughout the call until concluding with an extremely rapid final burst of pulses. Each pulse possesses four distinct frequency components and two separate subpulses; examination of expanded waveforms indicates that each pulse is also a brief descending frequency sweep.

We compare the mating calls of each species to other taxa in the previously-defined species group to which each belongs and we note call characteristics that uniquely diagnose each species. Call bioacoustics are

powerful techniques for studying species-specific behavioral and neurophysiological attributes of Philippine frogs; we expect that several more endemic Visayan species may be discovered in the near future through ongoing application of these techniques to problems in Philippine frog taxonomy and behavioral ecology.

Introduction

Philippine frogs of the genus Platymantis consist of 26 currently-recognized distinct species (Alcala and Brown, 1998, 1999) embodying a wide range of morphological, ecological, and behavioral variations. On the basis of morphology, this impressive Philippine radiation has recently been organized into several species groups (Brown et al., 1997a, 1997b; Alcala and Brown, 1999), each consisting of putative clades (sensu de Queiroz, 1999; Brown and Diesmos, 2001) of morphologically-cohesive and presumably closely-related species. To date, no phylogenetic appraisal of these species groups has been forthcoming, but preliminary results of a comprehensive phylogenetic analysis of the genus based on mitochondrial DNA sequence data (RMB, unpublished data) suggests that not all currently-recognized species groups are monophyletic (contain lineages all stemming from a single common ancestor). A full re-assessment of the taxonomy of this group must await the completion of that study.

One body of evidence that has been brought to bear on specific problems in platymantine frog taxonomy is acoustical analyses of male advertisement calls. Several recent studies (Brown et al., 1997b, 1997c, 1999) have demonstrated the value of studying species-specific acoustic signals for elucidation of species boundaries and identification of cryptic species. In these and related studies (Brown, Diesmos, and Alcala, unpublished data), analyses of patterns of mate-recognition signals have been crucial in identifying numerous unrecognized, new species, especially in the *P. dorsalis* species group (Brown et al., 1997a, 1997c, 1999). Continuing studies utilizing acoustic techniques should complement

previous work on morphological variation (e.g., Brown and Alcala, 1970a, 1982) in an effort to provide a comprehensive review of the Philippine members of the genus and to understand patterns and processes relating to the evolution of acoustical and functional diversity in advertisement calls of this diverse assemblage of Philippine endemics.

As part of this larger effort, we have recently conducted field studies of the behavioral ecology of Visavan species on the islands of Negros, Panay, and several smaller islets associated with these larger landmasses. This work has provided us with the opportunity to study the vocalizations associated with courtship behaviors of two threatened Visayan endemics: the celebrated Negros limestone cave frog, Platymantis spelaeus, and the poorly-known Gigante Island frog, P. insulatus (Fig. 1).

Platymantis spelaeus has a distribution limited to a few limestone outcrops on southern Negros Island (Brown and Alcala, 1982). Platymantis insulatus is a presumably relictual species limited to a few small islets (the Gigante Group) off the NE coast of Panay (Brown and Alcala, 1970a; Alcala and Brown, 1998; Brown and Alcala, 2000; Ferner et al., 2001).

Assessments of the conservation status of these species have been hampered by a lack of basic abundance, distributional, and natural history data, but recent efforts to arrive at a consensus regarding the conservation status of Philippine amphibians have considered both P. spelaeus and P. insulatus to be at some degree of risk of extinction. The actual category of risk assessment has ranged in different accounts from "vulnerable" to "critically endangered", but all parties involved do agree that this risk must primarily be due to habitat destruction in both species' restricted geographical ranges (Alcala and Custodio, 1995; Afuang and Gonzales, 1997; Banks, 1999; Brown et al., 2001; Diesmos et al., unpublished data). In this paper we provide the first published descriptions of the mate-recognition signals in these two threatened Visayan endemics, and we discuss in detail the differences between the species in numerous characteristics of their advertisement calls.

Materials and Methods

We visited the type localities of *P. spelaeus* (Fig. 2; Tiyabanan Barrio, Municipality of Basay; Brown and Alcala, 1982) and P. insulatus (Fig. 2; Gigante Island; Brown and Alcala, 1970a) during the months of May and June, 2001. We concentrated informal survey efforts on hours of the day immediately prior to and immediately following sunset (approximately 1800 h) at the beginning of the rainy season on days when the local area had received heavy rains. The advertisement calls of species were recorded at temperatures between 25 and 27°C, with a SonyTM WM DC6 Professional Walkman and a SennheiserTM ME80 condenser microphone (equipped with K3U power module). Calls were recorded at distances ranging from 1.5 to 2.0 m and ambient, cloacal, and substrate temperatures were taken immediately after acoustic recordings. Frogs were recorded, photographed, briefly captured by hand, weighed (to the nearest tenth of a gram [0.1] g]), measured (Snout-to-vent length [SVL to the nearest 0.1 mm]), and then released back into their original microhabitats.

Calls were digitized and analyzed using Soundedit[©] (Macromedia, 1995) and Canary[©] (Charif et al., 1996) software installed on a Macintosh computer. We examined oscillograms (waveforms), audiospectrograms (sonograms), and results of the Fast Fourier Transformation (frequency spectrum; FFT) for a variety of temporal and spectral characters. No temperature correction was undertaken during call analysis due to the narrow range of ambient temperatures recorded. Call rate and pulse rate were defined as: (total number of calls or pulses – 1) / time from beginning of first call or pulse to beginning of last.

Results

General observations

Platymantis spelaeus calls in large, loosely-congregated choruses, with the greatest concentration of courtship behavior

and reproductive activity in the evenings, following heavy rains. Choruses were subjectively characterized as relatively "loud" by observers who could clearly hear many calling frogs over high levels of ambient background noise during a rainstorm. Densities of calling individuals appeared to be relatively high; we subjectively estimated that between 10 and 30 individuals could be simultaneously heard by investigators at various areas in the type locality. Calling appeared to be concentrated in the several hours immediately following sunset on rainy nights. We observed frogs in small caves, around the mouths of caves and also farther from caves, on limestone hillsides, in disturbed regenerating scrubby vegetation, and calling from porous limestone boulders around the edges of fields.

Platymantis insulatus calls in small, more tightlycongregated choruses that were subjectively characterized as relatively "quiet" by observers. Observers had to strain to hear calling frogs against ambient background noise (undulating surf from a beach 20-30 m away). We only observed calling frogs on steep limestone hillsides and from karst cliffs at the sea's edge (Fig. 3). Calling activity was heard after sunset following a light rain and at dawn, again following rain. Densities of calling individuals appeared to be relatively low; we estimated that four to six individuals could be simultaneously heard by investigators at a given time in the areas we visited. On several occasions, individuals called from deep within porous limestone karst and in small caves that were inaccessible to us. Unlike nearly all other species of Philippine frogs, this species calls very close to the edge of the sea with high levels of ambient noise produced by the ocean's surf. This species appears to escape the extreme heat and aridity of the dry Gigante Island environment by retreating during the day into caves, cracks, and crevices in porous limestone karst.

Platymantis spelaeus

The mating call of *P. spelaeus* is a complex, tonal, whistling two-syllable call consisting of a higher frequency first note and a

lower frequency second note, each of similar duration. After initial single calls, *P. spelaeus* delivers paired, two-note calls with a brief pause before calling again (Fig. 4A). Calls sound to the human ear like the complex di-syllabic call of a small bird: "Pee-coh, pee-coh...pee-coh, pee-coh".

The following description is based on recordings of two individuals for which we secured high-quality recording segments of twelve and nine minutes continuous calling per individual (18 and 14 call bouts, respectively). During calling, the first individual called from a debris pile 45 cm above the ground, and the second individual called from a decaying tree stump, 30 cm above the ground (both 1.5 m from the microphone). The first individual's (49.1 mm SVL, 8.9 g) cloacal temperature was 27.6°C (25.3°C ambient, 25.3°C substrate) and the second's (41.3 mm SVL, 8.2 g) was 27.2°C (26.9°C ambient, 25.4°C substrate).

Call groups in the first frog were initiated with 2–4 (\bar{x} =2.8 ± 1.1 SD; n = 18) single calls of two notes each, followed by 2–5 (\bar{x} 3.3 ± 0.9 SD; n = 18) paired, two-note calls (i.e., paired calls had a total of four distinct notes). In the second frog, call groups were initiated with 2–4 (\bar{x} =3.0 ± 1.1 SD; n = 14) single-note calls followed by 2–5 (\bar{x} =3.4 ± 1.1 SD; n = 14) paired calls. Calling bouts lasted for 13.2–24.8 (\bar{x} =18.5 ± 3.2 SD; n = 18) s interspersed with 17.1–28.5 (\bar{x} =24.1 ± 5.4 SD; n = 17) s of silence in the first frog. Call groups lasted 11.1–23.3 (\bar{x} =17.9 ± 4.3 SD; n = 14) s in the second frog, interspersed with 15.1–25.7 (\bar{x} =18.4 ± 6.0 SD; n = 13) s intergroup intervals. Mean calling rate within bouts (including both single and paired calls) was 1.9 (± 0.09 SD; n = 18) call/s for the first frog and 1.7 (± 0.14 SD; n = 14) call/s for the second individual.

Mean call duration ranged from 130 to 138.2 (\overline{x} =128.2 ± 28.1 SD; n = 32 calls) ms for single calls and 348.6 to 380.1 (\overline{x} = 355±26.2 SD; n = 32 calls) ms for paired calls (from two individual frogs). Intervals between paired calls were shorter (\overline{x} =1.6±0.4 SD, range = 1.5–2.8 s; n = 32 calls) than those between single calls (\overline{x} =3.1±1.6 SD; range = 1.6–8.9 s; n = 32 calls).

The audiospectrogram depicts single calls of two distinctly different inverted U-shaped frequency modulated arcs (Fig. 4B): the first a nearly symmetrical arc, consisting of a pure tone rise and fall in frequency to a final frequency just below initial. By calculating the FFT throughout different portions of the call (not shown), we determined that, for the first individual, frequency of the first note invariably began a gradual rise from 2.2 kHz, to peak frequency of 2.4 at midnote (approx. 30 ms), followed by a gradual decline to below initial frequency at 1.9 kHz. In the second frog, the first note frequency arc rose from 2.4 to 2.8 kHz at midnote, then fell to a final frequency of 2.1 kHz.

The second note was invariably more complex, beginning with a rapid rise from ambient to nearly peak amplitude and with an initial rapidly-pulsed vibrational or amplitude-modulated element that was converted to a pure tone at mid-note (Fig. 4B). At the point where this note was transformed from vibrational to a pure tone, the first frog's peak frequency was 1.89 kHz; the second frequency arc then rose to a peak frequency at 2.1 kHz, before falling to a final frequency of 1.9 kHz. In the second frog, this second brief frequency arc rose from 1.7 to 2.1 kHz before declining to a final frequency of 1.9 kHz. In the audiospectrograms of the first note for most calls, one, two, or occasionally three faint but distinct harmonics are evident at frequency intervals that were clearly multiples of the fundamental (=emphasized) frequency.

Amplitude modulation evident in the oscillogram (waveform) for single two-note calls (as well as the first call in paired calls; see Fig. 4C) depicts two envelopes of nearly equal energy with a gradual, irregular rise to peak sound pressure levels corresponding to peak frequency, followed by a similar and opposite decline to ambient pressure. In single calls, the first note duration was greater than that of the second: in the first frog, mean first note duration ranged from 62.8 to 65.6 ($\bar{x} = 64.6 \pm 1.1 \text{ SD}$; n = 18) ms and in the second frog, first note duration was very similar, ranging from 60.9 to 64.3 ($\overline{x} = 63.4 \pm 1.1 \text{ SD}$; n = 14) ms. Second note total duration ranged from 50.1 to 55.8 $(x = 52.1 \pm 1.8 \text{ SD}; n = 18)$ ms in the first frog and from 50.8 to 56.5 $(\bar{x} = 53.0 \pm 2.1 \text{ SD}; n = 14)$ ms in the second frog. The first, amplitude modulated portion (invariably with five subpulses) of the second note ranged from 25.1 to 27.6 $(\bar{x} = 36.5 \pm 0.88 \text{ SD}; n = 18)$ and the second, frequency modulated portion of the second note ranged from 24.2 to 27.0 $(\bar{x} = 26.1 \pm 1.5 \text{ SD}; n = 18)$.

In paired calls of both individuals, we observed an imperfect duplicating of the single two-note call described above. In these calls the first and second call were distinctly different in a stereotyped manner. First, whereas the interval separating two-note single calls ranged from 8.9 to 13.8 ($\bar{x} = 12.2 \pm 3.6 \text{ SD}$; n = 32) ms and did not differ appreciably from internote intervals in the first call of paired calls (10.1 to $14.2: \bar{x} = 11.4 \pm 2.4 \text{ SD}$; n = 32), this same interval was consistently of longer duration in the second of paired calls. In the later case, internote intervals ranged from 31.3 to 47.4 ($\bar{x} = 38.1 \pm 3.8 \text{ SD}$; n = 32) ms. Also, in paired calls, mean first note duration in the second call was consistently shorter than mean first note duration in single calls (see above) ranging from 48.7 to 53.4 ($\bar{x} = 50.4 \pm 2.2 \text{ SD}$; n = 32).

Additional differences between first and second calls in paired calls are evident in the waveform (Fig. 4C). Although the first note of the second call is only moderately more audible to the human ear than that of the first, it is approximately 60% greater in relative amplitude. Additionally, both frequency and amplitude of the tonal portion of the second note decline between calls in paired calls. The decline in amplitude occurs as a nearly 40% loss of relative amplitude and, as discussed above, the peak frequency of the second note declines by about 10–20%. Finally, in paired calls, harmonic structure of the second call is more complex than that of the first (Fig. 4B); in these calls harmonic structure is relatively more rich than that of single calls as well, with up to five or sometimes six distinct harmonic multiples of the fundamental (vs. two to three) on the first note of the second call.

Platymantis insulatus

The advertisement call of *P. insulatus* is rapidly pulsed and highly amplitude-modulated, with a long series of brief clicking pulses, gradually increasing in pulse rate (corresponding to a decline in interpulse interval) throughout the call, until climaxing at an extremely rapid final burst of pulses (Fig. 5A). The rapidly-delivered brief clicks, interspersed with interpulse intervals of varying duration, sound, to the human ear, like the click vocalizations of a dolphin: "tik...tik, tik, tik, tik, tik-tik".

Our description is based on two separate recordings of one frog (recorded four minutes apart), of eleven and six minutes, six and four calls respectively. During the first recording, this frog called from a limestone rock, 15 cm above the ground, and during the second, it called from the edge of a limestone cliff, 30 cm from the ground, just above the rock perch of the first recording (both recordings 2.0 m from the microphone). This individual's (39.1 mm SVL, 4.9 g) cloacal temperature was 27.1°C (26.9°C ambient, 25.4°C substrate). For the analysis, we combined data from the two recordings and analyzed them together.

The *Platymantis insulatus* in our recordings called every 28-41 s, with a calling rate of 0.03 call/s across the total recording segment. Pulse rate within calls ranged from 4.1 to 5.3 ($\bar{x} = 4.6 \pm$ 0.8 SD; n = 10) pulse/s when averaged across the entire call, however, interpulse interval declined and pulse rate increased throughout the call (Fig. 6). Mean interpulse interval at the beginning (measured between 2nd-3rd pulse) of the call declined from 360 to 900 ($\overline{x} = 554 \pm 39.8$ SD; n = 10) ms to 63–97 ($\overline{x} = 74 \pm 7.9$ SD; n = 10) ms by the call's end (measured between penultimate and last pulse). Individual pulses ranged from approximately 15 to 25 ms and consisted of a near-instantaneous rise from ambient to peak amplitude, followed by a more gradual, approximately 10-20 ms decline back to ambient levels. Pulses appeared stereotyped and invariant, with only the first 2-4 pulses slightly lower (approximately 80-90%) than amplitude levels carried throughout the remainder of the call.

The power spectrum (Fig. 5 - not shown; calculated over the first few milliseconds of each pulse) allowed for the identification of four frequency components within each pulse. At the beginning of the call, these include distinct peak frequencies of 1.03 kHz (the fundamental), 2.07 (the second = dominant frequency), 3.1 (third harmonic) and 4.13 kHz (fourth harmonic). By the end of the call, peak frequency of all components increases slightly, with approximate peak frequencies of 1.2, 2.38, 3.57, and 4.78 kHz, respectively. Due to the brief duration of the pulse, these elements are barely visible in the audiospectrogram (Fig. 5B). Examination of the expanded waveform and audiospectrogram indicates that individual pulses are actually composed of two distinct subpulses, one at the beginning, and one at the end of shallow (2.4–2.1 kHz) frequency sweeps (Fig. 5B-C).

Discussion

Detailed studies of herpetological communities inhabiting isolated montane habitats, separate islands, or distinct geologic components of larger Visayan islands are warranted due to the fact that these environments appear to have contributed to the evolutionary process of speciation and often bear interesting faunal assemblages and distinct endemic species. Relatively few such detailed studies are available in the Visayas (but see Brown and Alcala, 1961, 1964, 1986, 1970b) but even simple faunal inventories (Ferner et al., 2001; Gaulke, 2001a, 2001b, 2001c) continue to produce some startling discoveries (Ferner et al., 1997, 2001; Brown et al., 1999, 2001; Gaulke and Curio, 2001; Gaulke, 2002).

Our descriptions of the vocalizations of these two endangered species should be of interest to herpetologists, behavioral ecologists, evolutionary biologists, and conservation biology specialists in the Philippines. In particular we urge future investigators to make use of advertisement calls during conservation and management studies for the purposes of population monitoring

and rapid-assessment censuses.

Our subjective characterizations of *P. spelaeus* choruses as "large, loosely-congregated, loud" calling aggregations and *P. insulatus* choruses as "smaller, tightly-congregated, quiet" aggregations require quantitative verification before they can be interpreted in a rigorous fashion. Data on natural frog densities, ambient noise levels, and absolute calling amplitude would all be a welcome improvement on our non-quantitative impressions reported here. Future studies of this sort should also focus on seasonal variation, meteorological conditions, habitat characteristics, and reproductive status of possible determinants of relative calling intensity.

Despite thetwo species' presumed common ancestry and numerous shared morphological and ecological attributes (Brown and Alcala, 1970a, 1982; Brown et al., 1997a, 1999), the mating calls of *Platymantis spelaeus* and *P. insulatus* are markedly different and share few characteristics in common. Relatively brief, complex calls with combinations of tonal frequency modulated notes and vibrational amplitude modulated notes are common to the *P. dorsalis* species group (*sensu* Brown et al., 1997a, 1997c), which includes *P. spelaeus*, whereas longer, highly pulsed, amplitude modulated calls are common to the *P. guentheri* species group (Brown et al., 1997a, 1997b; Diesmos, 1998), including *P. insulatus* (Alcala and Brown, 1998, 1999).

Other members of the *P. dorsalis* species group that possess two-note calls include *P. indeprensus*, *P. levigatus*, *P. pseudodorsalis*, *P. cagayanensis*, *P. mimulus*, *P. niomae* and several currently unnamed species awaiting formal taxonomic description. Other members of this complex possessing frequency modulated syllables as part of their call include *P. dorsalis*, *P. pseudodorsalis*, and a few unnamed species (Brown et al., 1997b, 1997c, 1999; Brown, Diesmos, and Alcala, unpublished data). Other *P. guentheri* group species with calls containing pulse rates approaching that of the terminal segments of the call of *P. insulatus* include *P. banahao*, *P. cornutus*, and several unnamed taxa

(Brown et al., 1999). Other *P. guentheri* group species possess either frequency modulated single note calls (e.g., *P. guentheri*) or slowly-delivered pulsed calls (*P. negrosenis*, *P. rabori*), some of which are composed of several individual brief frequency sweeps (e.g., *P. luzonensis*). A complete and detailed comparison of intra- and interspecific call variation in these and related species provides ground for future research (Brown, Diesmos and Alcala, unpublished data).

The paired two-note calls of P. spelaeus are unusually complex; among anurans, few other species possess calls comparable (Duellman and Trueb, 1986; Ryan, 1983; Cocroft et al., 1990; Brown and Iskandar, 2000). Although it is too early to ascertain the function of each of the elements of the call of P. spelaeus, in certain well-studied complexes (e.g. Ryan and Rand, 1993a, 1993b, 1993c), different call elements may be produced by distinct mechanisms and may function separately in species recognition, mate attraction, and/or territoriality (Blair, 1964; Duellman and Trueb, 1986). Additionally, the same characteristics of the male advertisement call of some species that are known to attract females (Ryan and Rand, 1993a, 1993c) not only provide cues to predators as to the location of calling males, but may contain information as to the caloric value of an individual calling male as a prey item (Tuttle and Ryan, 1982). Thus, it is conceivable that varying natural and/or sexual selective regimes may operate differently on different portions of the call. Similarly, it is conceivable that opposing selective forces may favor separate extremes in the range of variation in a single trait in separate contexts. It will be interesting to study the calls of both P. spelaeus and P. insulatus in further detail once additional recordings become available and further studies of the behavior of each species can be conducted in the field. A robust and independent phylogenetic estimate as an historical framework should make for particularly powerful comparative studies of acoustic, behavioral, and ecological variation in the future.

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Fig. 1— Platymantis spelaeus (above) and Platymantis insulatus (below) in their natural limestone habitats on S. Negros and Gigante islands (Fig. 2, 3), respectively.



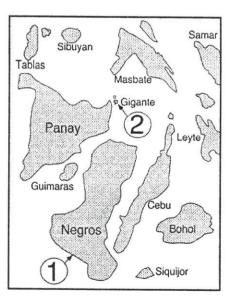


Fig. 2.— Type localities for the Visayan endemics *Platymantis spelaeus* (1: Negros Isl., Municipality of Basay) and *Platymantis insulatus* (2: Gigante Isl.).

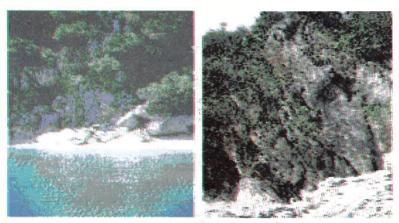


Fig. 3.— Habitat of *Platymantis insulatus* at the type locality, Gigante Island. Left, limestone karst cliff habitat jutting abruptly from the beach of Gigante North Island; right, details of porous limestone where *P. insulatus* specimens were recorded.

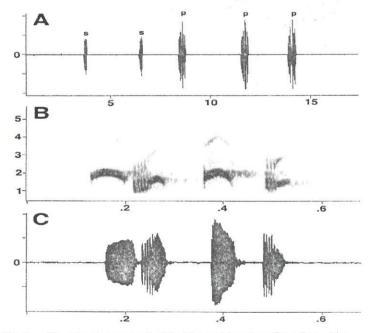


Fig. 4.— The advertisement call of the Negros Limestone Cave Frog, *Platymantis spelaeus*. (A) oscillogram (waveform: relative amplitude vs. time in s) of typical call group with two single ("s") and three paired ("p") calls; (B) audiospectrogram (sonogram: frequency in kHz vs. time in s), and (C) expanded waveform (relative amplitude vs. time in ms) of a typical paired call.

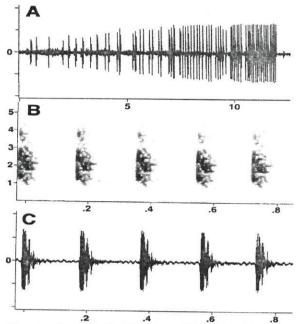


Fig. 5.— The advertisement call of the Gigante Island Frog, *Platymantis insulatus*:

(A) oscillogram (waveform: relative amplitude vs. time in s) of a typical 12 s call; (B) audiospectrogram (sonogram: frequency in kHz vs. time in ms) of five pulses, and (C) expanded waveform (relative amplitude vs. time in ms).

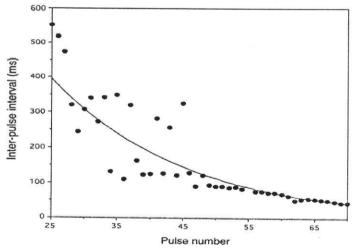


Fig. 6.— The relationship between pulse number and interpulse interval in one representative call of *Platymantis insulatus*.