

Nest Site Selection, Larval Hatching, and Advertisement Calls, of *Rana arathooni* from Southwestern Sulawesi (Celebes) Island, Indonesia

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ABSTRACT.—We provide information on the basic reproductive ecology, chorusing behaviors, and advertisement calls of *Rana arathooni* from southwestern Sulawesi, Indonesia. Nest sites in leaf litter and wet detritus are congregated on the steep banks of large, rapidly flowing mountain streams. When disturbed, hatchlings break free of the egg capsule and tumble down rocks or slide down muddy banks to the water below. The combination of choice of steep banks as nest sites and unusual behavior of the larvae suggests an unusual predator escape strategy. Larvae may avoid aquatic predators by extending development period on land but can rapidly evade predation and escape to the water below when threatened by terrestrial predators. Males form small choruses, with most individuals calling from under leaf litter and within the nest. The advertisement call of *Rana arathooni* is unusually complex and invariant and call structure is unique in that modulation of amplitude and frequency are inversely correlated.

Rana arathooni was described in 1927 from the village of Cikoro at the base of southwestern Sulawesi's tallest mountain, Mt. Lompobatang (Fig. 1; Smith, 1927). Despite Mt. Lompobatang's close proximity to Ujung Pandang (Sulawesi's largest city, formerly known as Makassar), the only mention of this species in subsequent publications has been its inclusion in biogeographical accounts, faunal lists, and surveys (Cranbrook, 1981; Whitten et al., 1987; Iskandar and Tjan, 1996).

Because the basic biology of most of Sulawesi's endemic species is not known, field studies should focus not only on taxonomic questions (e.g., Van Kampen, 1923; Iskandar and Tjan, 1996) but also on problems associated with the ecological, life history, and behavioral traits that may have played a role in the evolution of Sulawesi's diverse and highly endemic frog fauna. The same is true for previously known species that may be well represented in museum collections but for which few ecological or behavioral field studies are available. *Rana arathooni* is an example of one such species.

Related Bornean and Philippine species, *Rana palawanensis*, *R. leytenensis*, and *R. finchi* are known as "guardian frogs" (Inger and Stuebing, 1997) and have been documented calling singly from under leaf litter in primary forest. In these species, males typically guard nests of developing eggs and, in the case of *R. palawanensis* and *R. finchi*, transport hatchling tadpoles to water on

their back (Alcala, 1962; Inger, 1966; Inger et al., 1986; Inger and Stuebing, 1997). Alcala (1962) argued that the placement of *R. leytenensis* clutches on leaves and rocks above water allowed for tadpoles to be passively washed by rains into the stream below.

Warkentin (1995) demonstrated that *Agalychnis callidryas* embryos possess the ability to escape terrestrial predators by hatching early and dropping to water below suspended clutches when attacked by egg eating snakes. Furthermore, she argued adaptive plasticity allowed *A. callidryas* to assess and exploit predation risks trade-offs before and after hatching. To our knowledge, such plasticity has not been documented in southeastern Asian ranid frogs. Nor are there currently available accounts of the basic ecology, reproductive biology, or behavior of *Rana arathooni*. Herein, we report on reproductive behaviors, nest site selection, larval escape tactics, and advertisement call of this rare Indonesian species.

MATERIALS AND METHODS

We visited the type locality of *Rana arathooni* at Cikoro Desa (spelled "Djikoro" by Smith, 1927 and Frost, 1985), 1570 m above sea level, southwestern face of Mt. Lompobatang ("Bon-thain Peak", Frost, 1985) and surveyed the area and forested region above for amphibians and reptiles between 15 and 24 May, 1998.

We established an elevational transect from

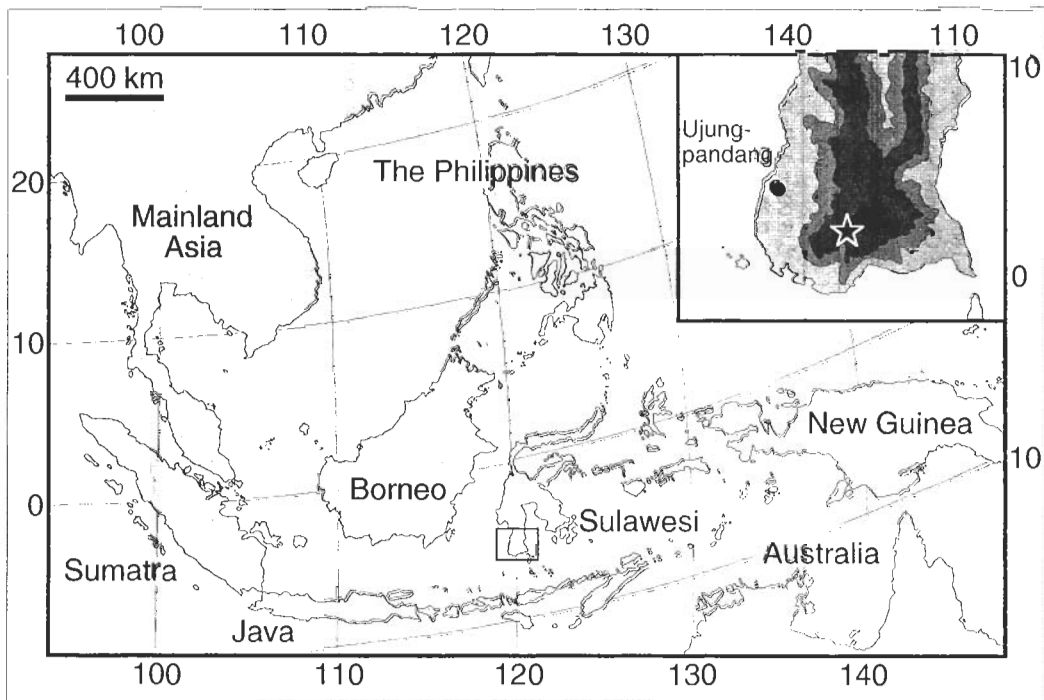


FIG. 1. Position of Sulawesi (Celebes) in relation to other major land masses at the Oriental-Australian faunal zone interface and (inset) the type locality of *Rana arathooni* (star) on the southwestern slopes of Mt. Lompobatang, south Sulawesi, Indonesia. Inset: discrete shades of darkness indicate 500 m elevational increments.

1580 to 1700 m above sea level and traversed its length two times per night. The transect crossed four small, fast-flowing mountain streams, 1.5–3.2 m in width. The survey conducted walking up the slope began nightly at 1700 h; the survey walking down the transect began at 2200–2330 h. Specimens of all anuran species were collected and identified (vouchers deposited in the Museum Zoologicum Bogoriense [MZB] and the Texas Natural History Collection of the Texas Memorial Museum [TNHC]; Appendix I).

We recorded the positions of choruses and the number of individuals calling per chorus (Table 1). Each chorus was observed for 10–25 min per night and one chorus (Chorus 3; Table 1) was observed in detail for 45–120 min per night on eight successive nights. In an effort to determine if physical characteristics of the stream bank and stream size are associated with calling activity and chorus size, we also recorded stream width, bank slope, and position of chorus above the water's surface. For simplicity, we examined correlations between these variables and numbers of calling individuals per chorus.

We recorded male vocalizations with a Sony WM DC6 Professional Walkman and a Sennheiser ME80 condenser microphone equipped with a K3U power module. Calls were recorded at distances ranging from 0.5–2.0 m and tem-

peratures (ambient, cloacal, and perch or clutch/nest) were recorded immediately after call recording. 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) for a variety of temporal and spectral characters. We also examined the general relationship between modulation of fundamental frequency and amplitude by performing a Fast Fourier Transformation at 5 ms intervals throughout expanded waveforms of individual notes. We scored dominant (=fundamental) frequency and relative amplitude directly from frequency spectrum and, for clarity of presentation, we examined simple correlations between frequency and relative amplitude for a single 15-note call.

Embryos and larvae were staged by comparison to the Gosner table of normal development (Gosner, 1960). There is no generally accepted taxonomy for southeast Asian ranids (Inger, 1954, 1966, 1996; Dubois, 1992). We follow Inger (1996) and Inger and Tan (1996) and include *arathooni* in the genus *Rana* pending taxonomic work in progress.

TABLE 1. Number of calling individuals of *Rana arathooni* at six choruses centered on four streams on Mt. Lompobatang, southwestern Sulawesi. Entries (mean \pm 1 SD; range) are summaries of eight nights of observations recorded by investigator walking up an elevational transect (1580–1700 m; 1700–1800 h) and those recorded by investigator walking down the same transect (1700–1580 m; 2200–2330–2300–2430 h). Numbers in parentheses following Stream No. are Chorus No. when multiple choruses were detected \pm 100 m up and down stream from crossing.

	Stream No. (chorus number)					
	1(1)	2(1)	3(3)	3(4)	4(5)	4(6)
No. males calling (up transect obs.)	0.38 \pm 0.52; 0–1	2.88 \pm 0.83; 2–4	5.50 \pm 2.51; 0–8	0.88 \pm 0.64; 0–2	5.13 \pm 0.64; 4–6	3.00 \pm 1.41; 0–4
No. males calling (down transect obs.)	0.38 \pm 0.52; 0–1	2.13 \pm 0.83; 1–4	5.25 \pm 2.05; 1–8	0.50 \pm 0.54; 0–1	5.25 \pm 0.88; 4–6	2.23 \pm 1.73; 0–5
Stream width at chorus location (m)	1.5	2.1	2.5	1.5	3.2	1.7
Chorus distance from stream (m)	5.1–6.0	8.0	1–2	3–3.5	1.2–1.6	3–3.5
Bank slope at chorus	10°	5°	80°	60°	60–70°	45°
Chorus height above water's surface (m)	0.05	0.05–0.15	2.0–3.5	0.7–1.1	2.0	1.6–2.0

Habitat and Chorus Locations.—The immediate surroundings of Cikoro Desa (at about 1500 m; Smith, 1927) have been deforested since the time of the discovery of *Rana arathooni* (Whitten et al., 1987), but intact, upper mid-montane closed-canopy climax rain forest (sensu Whitmore, 1984; 1996) persists from 0.5 km above the village, starting at 1570 m (RMB, pers. obs.; Fig. 2). Dominant canopy vegetation in the area where *R. arathooni* were observed predominantly consisted of *Pinus* spp., *Shorea* spp., *Dipterocarpus* spp. and *Lithocarpus* spp. (some *Ficus* spp. sapling were identified) and understory vegetation include *Calamus* spp., *Areca* spp., *Pandanus* spp., and *Freycinnetia* spp. Epiphytic orchids, mosses, and ferns (*Asplenium* spp. and *Dicranopteris* spp.) were abundant. The moon was waning for the final week of our stay at Cikoro (no moon on the night of 26 May 1998).

Other anurans observed at this site and in Cikoro Desa included *Bufo celebensis*, *Limnonectes microtympanum*, *Oreophryne variabilis*, and an unidentified species of *Rhacophorus*. Other species observed (by DTI) or reported (VanKampen, 1923; Iskandar and Tjan, 1996) near the base of Mt. Lompobatang include *Bufo melanostictus*, *B. biporcatus*, *Rana cancrivora*, *Rana cf palawanensis*, *Rana celebensis*, *R. raniceps*, *R. erythraea*, *Occidozyga semipalmata*, *O. celebensis*, *Rhacophorus edentulus*, *R. monticola*, *Polypedates leucomystax*, *Kaloula baleata* and *K. pulchra*.

Two groups of frogs were detected at Streams 3 and 4, while only single calling males were observed on some nights at streams 1 and 2 (Table 1). Number of calling males ranged from 0–1 at Chorus 1, 5–8 at Chorus 3, and 4–6 at Chorus 5. On a single night (15 May) there was little or no activity at Chorus 3; exclusion of this apparently aberrant night brings mean number of calling males to 6.28 (± 1.27 SD; 5–8) and 5.82 (± 1.21 SD; 5–8) for up-transect and down-transect observations respectively (Table 1). Low sample sizes prevent rigorous statistical verification of apparent trends, but correlation coefficients describing the relationship between the number of calling males and bank slope ($r = 0.60$), stream width ($r = 0.71$), and chorus height above the surface of the water ($r = 0.81$) are all generally positive (Fig. 3A–C). This confirms our qualitative assessment that calling activity was centered on steep-banked slopes of larger streams with choruses situated relatively high (about 1.0–3.5 m) above the surface of the stream. Chorus activity also was qualitatively characterized as being positively associated with the loudest of local environments (in spray zones near fast-moving, cascading rapids in streams on steep slopes, where observers had to



FIG. 2. Male attendance of nests in *Rana arathooni* (above: TNHC 59087, SVL = 29.9 mm; mass = 2.9 g; clutch TNHC 59311, N = 21 embryos) and vegetation characteristics (below) in forested habitat at 1600 m. (upper mid-montane rainforest) near the type locality of *Rana arathooni* Smith, 1927 (Cikoro Desa, Mt. Lompobatang, southwestern Sulawesi Island, Indonesia). Photographs by Rafe M. Brown.

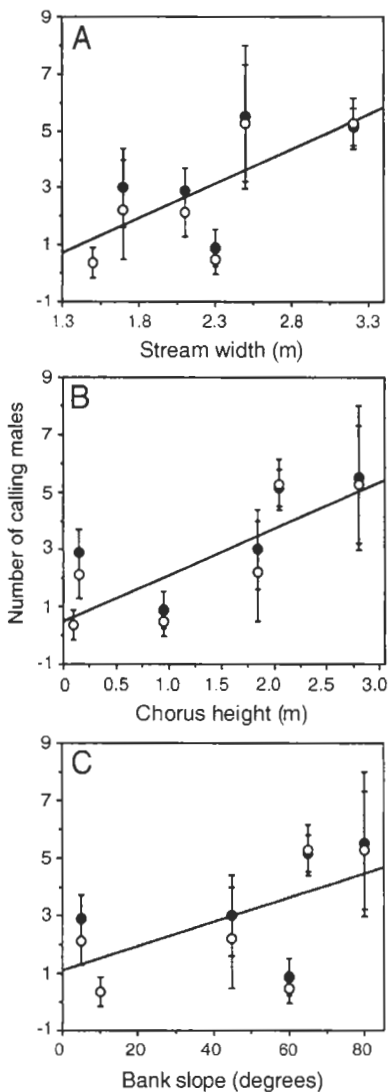


FIG. 3. Relationship between number of calling males and (A) stream width ($r = 0.71$), (B) chorus height above the surface of the water ($r = 0.81$), (C) and stream bank slope ($r = 0.60$). Shaded circles represent mean number of calling males recorded on eight consecutive nights by investigators traversing up the transect (see text); open circles are the same observations recorded while traveling down the transect. Error bars = 1 SD. Lines were added to emphasize the correlations only and do not represent fitted slopes or regression equations.

shout to communicate). Smaller, slowly moving streams with shallower banks in quieter regions of the nearby forest did not support larger choruses (Table 1), and intense searches of leaf litter in these areas generated no frogs or nests.

Individual Activity, Nest Site Selection, and Larval Escape Tactics.—Chorus 3 usually consisted

of 5–8 calling males and at least three females. The chorus was located on an extremely steep slope, close to the water's edge, and relatively high above the surface of the rapidly flowing near-by stream (Table 1). Frogs called from cracks in the rocks bordering the stream (one frog visible to observers on three successive nights), from muddy holes in the bank (two frogs visible 10–15 cm deep on three nights), and from under 4–10 cm of leaf litter, moss, and rotting roots from within terrestrial nests with developing embryos (Fig. 2; 3–6 frogs, hidden under leaf litter, on all seven nights). On five nights, non-calling males were observed in rocks and holes. Only when at least three males were calling from under leaf litter did frogs in holes and cracks participate in the chorus. During these times, three females were regularly seen moving through the leaf litter and approaching males. We did not observe males moving from nests or perches, and no amplexus, fertilization, or egg deposition were observed.

Most males called from terrestrial nests under forest floor detritus (Fig. 2). Nests containing 10–29 eggs ($\bar{x} = 21.3 \pm 4.5$ SD; $N = 9$), were located 1.6–3.0 m ($\bar{x} = 2.7 \pm 0.7$ SD; $N = 9$) from and 1.0–3.5 m ($\bar{x} = 2.5 \pm 0.9$; $N = 9$) above the stream, and were covered by 6–10 cm of spray-soaked leaf litter detritus. Two clutches (TNHC 59312–13) of 29 and 17 embryos were each estimated at Gosner stage 8–9, and two other clutches (TNHC 59311, 59324) of 21 and 17 embryos were at Gosner stage 21–24. Hatchlings (TNHC 59311, 59324) possess a well-developed cornea, a muscular tail with aggregated melanophores, and an obvious vent but lack functional mouthparts, and have no external gills, or visible open operculum. We found four nests at Chorus 3, two at Chorus 4, one at Chorus 5, and two at portions of stream banks with no apparent chorus actively present (22 and 26 eggs respectively). We observed males in nests calling from perches on top of egg masses ($N = 4$) or slightly to one side (≤ 5 cm; $N = 7$) of the clutches.

When we attempted to collect clutches with well-developed embryos, Gosner stage 21–24 hatchling tadpoles began rapid erratic movements within the egg and within several seconds broke free of the egg capsule, wriggled energetically out of the nest depression, and slid or tumbled 1.5–3.5 m down the steep stream embankment directly into the rapidly flowing water. Two tadpoles escaped collection in one clutch by wriggling out of their nest and bouncing down the steep slope created by a large rock. At two other clutches, disturbed tadpoles simultaneously erupted from eggs in a coordinated fashion and escaped collection by sliding

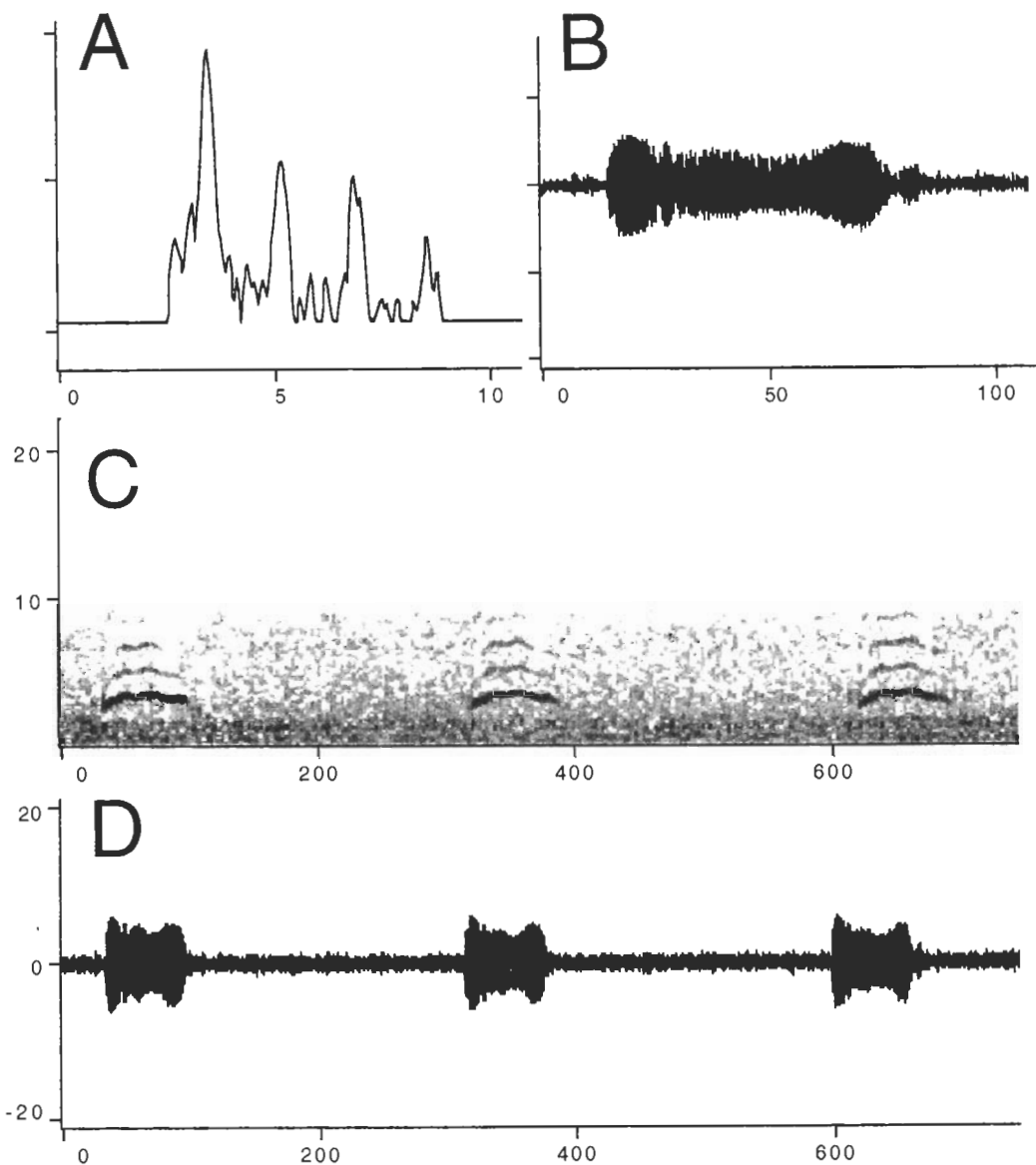


FIG. 4. (A) Frequency spectrum (FFT: relative amplitude vs. frequency in kHz), (B) expanded waveform (relative amplitude vs. time in ms), (C) audiospectrogram (sonogram: frequency in kHz vs. time in ms) and (D) oscillogram (relative amplitude vs. time in ms) of one rapid burst (included for simplicity; usual mean call rate = 2.2 ± 1.5 SD; $N = 8$; range = 1.1-2.3) of notes in the advertisement calls of *Rana arathooni* (TNHC 59087) at the type locality on Mt. Lompobatang. The FFT, expanded waveform, and oscillogram are based on the third note shown in the audiospectrogram. These three notes were the first in a 15 note call (see text). Call was recorded from a distance of 0.7 m; ambient air temperature = 16.0°C ; frog temperature = 16.1°C ; 19 May 1998, 2000 h, by Rafe M. Brown.

down steep, water logged, muddy stream banks and rivulets created by water draining from the steep banks into the larger stream below.

Extensive search efforts for tadpoles in the stream (under rocks, in eddies, side pools, under leaf litter, in sandy and muddy portions of stream bed) failed to produce tadpoles of *R. ar-*

athooni (though *Limnonectes* tadpoles in a variety of stages were very abundant).

Advertisement Calls.—In general, the audiospectrogram depicts calls that consist of singly repeated frequency modulated notes (with three to four harmonics; Fig. 4A, C) sounding to the human ear like a series of shrill “bleats” (Smith

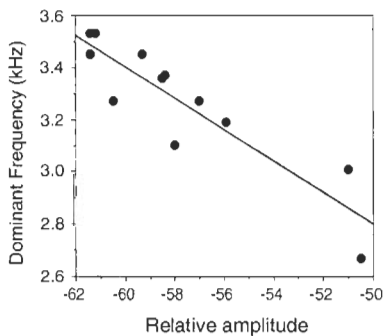


FIG. 5. The relationship between dominant (=fundamental) frequency and relative amplitude (arbitrary units) for a single representative *Rana arathooni* note ($r = -0.89$) in a 15 note call. Amplitude and frequency were measured at five ms intervals throughout the note shown in Fig. 4B. See Materials and Methods for further details.

1927) that form a shallow, slightly asymmetrical, inverted U-shaped convex frequency arc (Fig. 4B, D). In general, the oscillogram depicts a concave, U-shaped waveform that declines from peak amplitude into a shallow concave trough, then rises to peak or near peak again by the end of the note. The striking pattern that emerges is an inverse relationship between frequency and amplitude (Figs. 4–5). Correlation coefficients describing this general trend ranged from -0.4 to -0.9 ($\bar{x} = -0.67 \pm 0.13$; $N = 12$).

Recorded calls (of TNHC 59087; 29.9 mm; 2.9 g; recorded from a distance of 0.7 m; ambient air temperature = 16.0°C ; cloacal temperature = 16.1 ; stream temperature = 15.7) were delivered in 8 bouts of calls (inter-call interval $\bar{x} = 26 \pm 10.6$ SD; 10 – 42 s) ranging from 8 to 17 notes ($\bar{x} = 12.5 \pm 2.9$ SD) per call. Rate of note delivery within calls ((total number of notes–1)/time from beginning of first note to beginning of last note) ranged from 1.1 to 2.3 notes/s ($\bar{x} = 2.2 \pm 1.5$ SD; excluding rapidly-delivered burst of two to four notes at the beginning of some calls).

The following descriptions of characteristics of individual calls are based on the third call recorded for male TNHC 59087 (2000 h). This is a 15-note call in which ambient noise was reduced relative to other calls recorded at the time because of a large tree trunk between the calling frog and nearby stream. During the recording, male TNHC 59087 was calling from a terrestrial nest and was situated on top of a clutch of eggs (Fig. 2). Note length ranged from 56–65 ms ($\bar{x} = 60.0 \pm 2.80$ SD; $N = 12$) and inter-note interval (excluding rapid burst of notes that commence this call) ranged from 530–540 ms ($\bar{x} = 536.9 \pm 4.0$ SD; $N = 12$).

Frequency modulation of the fundamental (=dominant) frequency of individual notes con-

sists of a convex sloping frequency sweep from 2.91–2.98 kHz ($\bar{x} = 2.93 \pm 0.03$ SD; $N = 12$) at the start of each note, to a peak frequency between 3.01 and 3.40 kHz ($\bar{x} = 3.38 \pm 1.0$ SD; $N = 12$) at midnote (rise time $\bar{x} = 18.20$ ms ± 0.30 SD; $N = 12$), then a convex arcing decline back to 1.91–2.60 kHz ($\bar{x} = 2.14 \pm 0.22$ SD; $N = 12$) at the very end of the note (decline time $\bar{x} = 6.3$ ms ± 0.16 SD; $N = 12$).

Individual calls are amplitude-modulated and the expanded call waveform (Fig. 4B) depicts a concave amplitude envelope. Notes consist of a rapid, 1.0–1.3 ms ($\bar{x} = 1.2 \pm 0.09$ SD; $N = 12$) rise in amplitude from ambient to a peak, a prolonged concave slight fall in intensity to about 65–75% (relative to peak amplitude) at midnote, a rise in amplitude back to peak pressure levels, and a rapid, 1.0–1.4 ms ($\bar{x} = 1.14 \pm 0.09$ SD; $N = 12$) drop in amplitude to ambient levels. In most notes (approximately 80%) there is a brief (3 ms) secondary pulse in amplitude (85% relative peak amplitude) immediately after the initial decline from peak to 65–75% (mid-note). In these same calls, there is another brief (6 ms) final amplitude subpulse (15% of relative peak amplitude) added to the end of the note following the decline to ambient pressure levels (Fig. 4B). Most of the energy in the call (peak intensity of the FFT; Fig. 4A) is partitioned into the fundamental frequency that peaks between 3.01 and 3.40 kHz ($\bar{x} = 3.38 \pm 1.0$ SD; $N = 12$); the first harmonic exhibits a peak frequency range from 5.01 to 5.10 kHz ($\bar{x} = 5.07 \pm 0.11$ SD; $N = 12$; approximately 60% relative intensity of the emphasized frequency) the second between 6.73 and 6.79 kHz ($\bar{x} = 6.76 \pm 0.02$ SD; $N = 12$; 54% relative intensity of the emphasized frequency), and the third between 8.40 and 8.50 kHz ($\bar{x} = 8.45 \pm 0.04$ SD; $N = 12$; 48% relative intensity of the emphasized frequency). A faint fourth harmonic was occasionally detected between 8 and 10 kHz.

DISCUSSION

We have documented male attendance of terrestrial nests in the poorly-known *Rana arathooni*. Similar behaviors have been observed in related Bornean populations referred to *R. palawanensis* and *R. finchi* (Inger and Stuebing, 1997). These species are known to call from under leaf litter in primary forest and males attend developing eggs through most of the larval period (Inger, 1966; Inger et al., 1986). However, both of these species differ from *R. arathooni* in that they call singly from the forest floor and do not form tight choruses on stream banks as observed in the present study. Additionally, these two species carry their tadpoles to water at the end of the larval period (Inger, 1966, 1985; Inger et al., 1986; Emerson, 1996; Inger and Stuebing,

1997. Similar terrestrial nest attendance has also been reported for Philippine *R. leytenis* (Alcala, 1962).

We have also documented an apparent mechanically-stimulated predator escape tactic that may allow larvae to escape to nearby running water when threatened by terrestrial predators. Although no natural terrestrial predators have been observed, the placement of the nests, coupled with the fact that tadpoles were difficult to collect while sliding and tumbling down stream banks all suggests an effective predator escape tactic. Similar larval escape tactics have been observed in rhacophorids (Inger, 1954, 1966; Alcala and Brown, 1956; Alcala, 1962; Brown and Alcala, 1982), ranids (Alcala and Brown, 1956; Alcala, 1962; Inger, 1966; Brown and Alcala, 1982), and hylids (Warkentin, 1995). In some of these cases, eggs are suspended on leaves (hylids) or deposited in a foam nests (rhacophorids) over water and tadpoles drop to the surface of the water when mature or threatened by predators (Alcala, 1962; Warkentin, 1995). Other reports of terrestrial nests of indirect developers involve longer distances from water and guidance or carrying of tadpoles to water by either sex (Inger, 1966; Watson and Martin, 1973; Lynch et al., 1983; Inger and Stuebing, 1997; Kaminsky et al., 1999). Alcala (1962) described tadpoles wriggling to water after hatching in the related *Limnonectes visayanus*, and Oldham (1977) has described similar behaviors in hyperoliids. Except *R. leytenis* (Alcala, 1962), we are unaware of other cases of nest site selection by adults that would apparently maximize the probability of successful sliding and tumbling of tadpoles to water after emergence from the eggs.

Warkentin (1995) described an apparent case of adaptive plasticity in timing of larval hatching in *Agalychnis callidryas* in response to predation risk trade-offs before and after hatching. Warkentin (1995) showed that *A. callidryas* maintains developmental plasticity in time of hatching from the egg capsule. This enables larvae to maximize development out of water and avoid aquatic predators or truncate the larval period and escape to water if threatened by terrestrial predators. Warkentin (1995) demonstrated that *A. callidryas* tadpoles' vulnerability to aquatic predators declines with subsequent maturation in the water. Furthermore, in the absence of terrestrial predators, larvae will lengthen the larval period out of water, presumably to maximize body size and increase their chances of survival after shifting to the aquatic niche. The cost associated with evading terrestrial predators is an increased susceptibility to aquatic predators by hatching early and at a smaller body size. While there are striking similarities between Warken-

tin's (1995) study and our observations of *Rana arathooni*, we have not determined if *R. arathooni* exhibits the same kind of adaptive plasticity in ontogenetic niche shifts as in *A. callidryas*, or if predation risk trade-offs before and after hatching are important in this species. An additional potential cost of a niche shift to the rapidly flowing streams on Mt. Lompobatang might include the risk of being swept away to a lower elevation habitat that is less suitable for larval development.

It is not clear whether temperature (22–26 C), humidity (unrecorded but likely $\geq 70\%$), slope (45–80°), or stream width (1.5–3.2 m) are primary determinants of nest site choice, but we suspect that slope and humidity may be particularly important. Nest site microhabitats have the highest local humidity (potentially advantageous for the development of terrestrial eggs) because of the spray from nearby rapidly running streams. Additionally, the steep slopes at these nest site locations may provide some protection from rising water that might be expected to wash away nests situated on flat or shallow stream banks. Finally, choice of a steeply sloping nest site may allow for larval escape by hatching if nests are threatened by terrestrial predators (e.g., Warkentin, 1995).

As noted, calling *Rana arathooni* were invariably associated with the loudest of local microhabitats. Similar observations recently have been reported for *Centrolene geckoideum* (Grant et al., 1999) and *Smilisca sila* (Tuttle and Ryan, 1982), species that call predominantly or exclusively from local environments of consistently high-intensity background noise. Despite being delivered underneath leaf litter next to a loud cascading stream, the calls of *R. arathooni* transmitted well enough for the chorus to be detected by the human ear well over 30 m from the source. The sound intensity of the rapidly cascading stream could be heard over 100 m from the source. In addition to the complex surrounding habitat (dense forest is known to attenuate and degrade calls; Ryan and Brenowitz, 1985; Ryan et al., 1990) and intense background noise from cascading streams, *R. arathooni* call at or below the ground's surface. This suggests that expected high degrees of call attenuation and degradation may pose a challenge to acoustic communication in this species. If nest (and call) site choice is limited by selection for increasing probability of larval survivorship, adult avoidance of visually-oriented predators (Tuttle and Ryan, 1982), proximity to water (Alcala, 1962), and high relative humidity, the high sound intensity environments of cascading streams may represent an associated constraint on acoustic communication. Nevertheless, *R. arathooni* delivers highly structured, non-random calls with lit-

tle temporal or spectral variation. The presence of well-organized call structure in this species contrasts with observations involving centrolenids that call in similar loud environments (Grant et al., 1999). In that study, an apparently random call structure (and implied lack of information content) was attributed to intense ambient noise of waterfalls and cascading streams. Grant et al. (1999) suggested that detailed temporal and spectral characters may be lost or degraded by background noise and thus may not be emphasized or maintained by selection in *Centrolene geckoideum*. In *R. arathooni*, the call structure is remarkably complex and invariant, suggesting continued selection for temporal and spectral call characters and information content in the advertisement call (Ryan, 1983; Ryan and Rand, 1993a). Effective communication in *R. arathooni* may be facilitated by close proximity between individuals (choruses consisted of individuals less than 4 m apart) and the redundant nature of call transmission. It would be interesting to determine if males and females exhibited positive phonotactic responses to frequencies common to the noise of cascading mountain streams—and thus might initially be attracted to choruses and nest sites by the sound of rapidly flowing and cascading water.

The unexpected inverse relationship between call frequency and amplitude modulation detected in this study contradicts most earlier reports known to us. In most species, if a relationship exists, frequency and amplitude modulation are of the same sign if not significantly positively correlated (i.e., *Physalaemus* species; Dudley and Rand, 1991; see Fig. 4 in Ryan and Rand, 1993b). Because of this unusual call structure, *R. arathooni* may constitute a particularly interesting model species for future studies of sound production and call mechanics in anurans.

Acknowledgments.—We thank the Research and Development Centre for Biology of the Indonesian Institute of Sciences (LIPI) and the Museum Zoologicum Bogoriense for their assistance in facilitating necessary permits. For logistical assistance, advice, field assistance, and other help, we thank S. Prijono, M. Sancoyo, H. Kurniati and I. Sidik (MZB), N. Babo, A. Bakry (Sulawesi Natural Resources Conservation Information Center), L. Ruedas, J. Froehlich, and R. Dickerman (University of New Mexico), Y. Andyani and Y. Supriatna (University of Indonesia, Depok), D. Byrnes (University of Wisconsin), and F. Yuwono. We are particularly grateful of M. Sancoyo's assistance with accessioning specimens, provision of data, and MZB catalog numbers. Support for R. Brown's field work was provided by the Society for the Study of Am-

phibians and Reptiles, the American Society of Ichthyologists and Herpetologists, The Explorers Club, The Section of Integrative Biology of the University of Texas at Austin, The Texas Memorial Museum, and by National Geographic Grants (No. 6177-98 to J. Froehlich and L. Ruedas and No. 5606-96 to R. Dudley and J. McGuire). Comments on preliminary drafts of the manuscript were provided by D. Cannatella, R. Dudley, A. Gluesenkamp, C. Infante, L. Ruedas, R. de Sá, and anonymous reviewers.

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Accepted: 21 April 2000.

APPENDIX 1

Specimens Examined

Rana arathoimi.—Indonesia, Sulawesi Island (Celebes); Sulawesi Selatan (South Sulawesi Province) Kabupaten (regency) Gowa, Kecamatan (kingdom) Tompo Bulu, Cikoro Desa (village of Cikoro), Dusun (township) Lembang Bune, Kampung (neighborhood) Parang Bintolo; 1570 m, Mt. Lompobatang; TNHC 59087 (Field No. RMB 1247, male, collected on clutch TNHC 59311), 59088 (RMB 1251, male, collected on clutch 59313 with female), 58916 (RMB 1250, female, collected with male 59088 on clutch 59313), 59106 (male, RMB 1329); 59105 (RMB 1249, male, collected with clutch 59312), MZB Amph. 3594 (RMB 1248, female, collected with clutch TNHC 59324), MZB Amph. 3595 (RMB 1309, female, collected in empty nest).