TADPOLE AND CALL OF *RANA TAIPEHENSIS* IN TAIWAN

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ABSTRACT—Both external and internal features of larval *Rana taipehensis* indicate a typical bottom feeder or mid-water dweller among dense aquatic vegetation in ponds. The tadpoles feed on a broad spectrum of food sizes and types, including soil and detritus. The call is a faint, whistle-like, single note that usually constitutes a component of rapid, repeated long series in an active chorus, or occasionally there are slow short series emitted alternately with long series. The fundamental frequencies of notes in long and short series range from 1.8-4.0 and 1.3-2.4 kHz respectively. Previous confusion of the larval morphology is clarified, and the acoustic features of two remotely isolated populations are compared.

KEY WORDS: Tadpole, Vocalization, *Rana taipehensis,* Ranidae, Anura

INTRODUCTION

Rana taipehensis is a poorly known species in Taiwan. Widely distributed in southern China, central Vietnam and eastern India, the frog is restricted to the northern and southern extremes of Taiwan, presumably because of severe habitat fragmentation caused by human activities (Chou, Chang and Lue, 1993). The call and tadpole were briefly described (Pope, 1931; Wallace, 1937; Liu and Hu, 1961) from localities in China, but the biology of this rare and vulnerable species remains largely unknown in Taiwan. Frogs in northern Taiwan occur in rice paddies, ponds and tea plantations in the spring, and tadpoles are found in the rice paddies with newly planted rice (Lue and Chen, 1982).

I present data on the morphology, microhabitat preferences and food items of the larvae and acoustic features of the adults. Confusion of the larval morphology described by Pope (1931) and Liu and Hu (1961) is clarified, and the acoustic features of two remotely isolated populations in Taiwan are compared.

MATERIALS AND METHODS

A description of the larval morphology of *Rana taipehensis* was based on three, stage 31 (Gosner, 1960) tadpoles reared from eggs laid by an amplectic pair (Kungputze, ca. 5 km north of Tamsui, Taipei County; 25° 13′ 54″ N, 121° 27′ 42″ E; ca. 100 m of elevation) and 10 tadpoles from Fawan (ca. 8.5 km south of Liangshan, Pintung County; 22° 38′ 04″ N, 120° 37″ 07″ E; ca. 100 m of elevation; Figure 1). Both groups of tadpoles are basically identical in morphology. Tadpoles in Gosner (1960) stages 31-38 were available.

External and internal features and gut contents were examined, and toluidine blue was used to add contrast to transparent tissues. Larval descriptions follow Inger's (1985) format and terminology with minor modifications from Altig (1970) and Wassersug (1976).

Calls were recorded (6 males at Kungputze, 3 males at Fawan) with a Sony TC-D5M cassette recorder. A Byeredynamic M 300N(c)S microphone at a distance of 30-40 cm from the calling males was used at Kungputze. At Fawan, a Sony condenser microphone (C-76) was used at a distance of about 1 m from the frogs. Air temperatures were recorded

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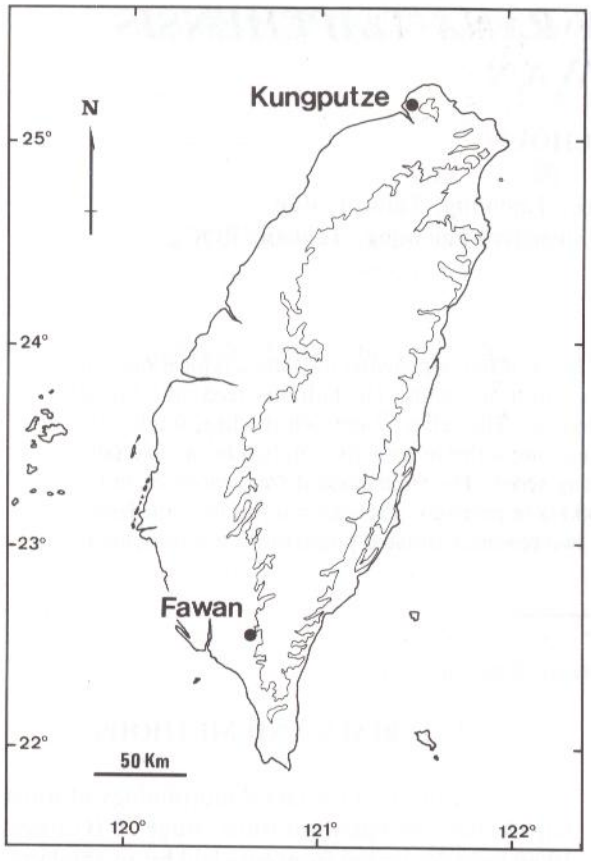

Figure 1. Map of Taiwan, showing sampling localities Kungputze and Fawan. The contour line is at 500 m.

near the frogs. Calls were analyzed with a KAY 5500 DSP Sona-Graph and sonograms were printed by a Kay 5510 Grey Scale Printer. Terminology of calls follows Duellman and Trueb (1986).

RESULTS

NOTES ON ECOLOGY AND DIETS

Lue and Chen (1982) stated that larval *Rana taipehensis* were common in rice paddies near Tamsui, but I could not locate tadpoles at Kungputze during several trips between April and September 1991. All the tadpoles obtained from the field were collected among the roots of water lettuce (*Pistia stratiotes*) from a permanent pond at Fawan.

In the lab, the tadpoles were kept in an aquarium containing 25 cm of water and water lettuce. Tadpoles rested on the bottom or among the long roots about 4 cm from the water surface. Occasionally, tadpoles hung vertically on the roots by the labial teeth or papillae. Disturbed tadpoles hid themselves among the bottom debris. The tadpoles were well camouflaged when they hid within the bottom debris.

Particles in the food traps and esophagus contained mainly soil, ooze and fragments of plant tissues. Also micro-organisms e.g., unicellular, colonial and filament-like green algae (*Spirogyra* and *Oedogonium*), various forms of diatoms, small-sized invertebrates and other unidentified organisms were found. These food items were found around the roots of water lettuce and near the soil.

Animal tissues were not found in field-preserved tadpoles, but tadpoles ate dead animals in the lab. Two larval *Rana taipehensis* (stages 35 and 37, HBL 11.1 mm and 12.6 mm respectively) presented with a freshly killed tadpole of *Polypedates megacephalus* (stage 28; HBL 14.3 mm) began to eat the tadpole within 5 min. The entire skin was grazed by the next day, and the body eaten by the third day. In a small aquarium ($20 \times 12 \times 10$ cm) filled with pond water and containing floating fern (*Salvinia natans*), tadpoles of *R. taipehensis* (N = 4), *R. latouchii* (2) and *Microhyla heymonsi* (4) co-existed for a month with no cases of cannibalism.

LARVAL MORPHOLOGY

External features.--Head-body elongate (HBL 9.4-10.9 mm, stages 31-38), slightly guitar-shaped in dorsal view (Figure 2), rounded at snout; width at spiracle 0.46-0.55 of head-body length; height 0.82-0.95 of width; eyes dorsolateral, part of cornea visible from below, above the longitudinal body axis; eyeball diameter 0.15-0.16 of head-body length; interorbital 1.32-1.60 times eyeball diameter, almost equal to eye-snout distance; nostrils open, small, dorsolateral, rim not raised, nasolacrimal duct not visible; snout-naris distance subequal to eye-naris; internarial subequal to interorbital distance. Oral disc (Figure 3) emarginate, ventral, subterminal, width 0.34-0.42 of body width at spiracle; upper labium with wide medial gap and with short papillae at corners; lower labium with continuous papillae in two rows with some short papillae between inner and outer rows near corners, outer row longer than inner; labial tooth row

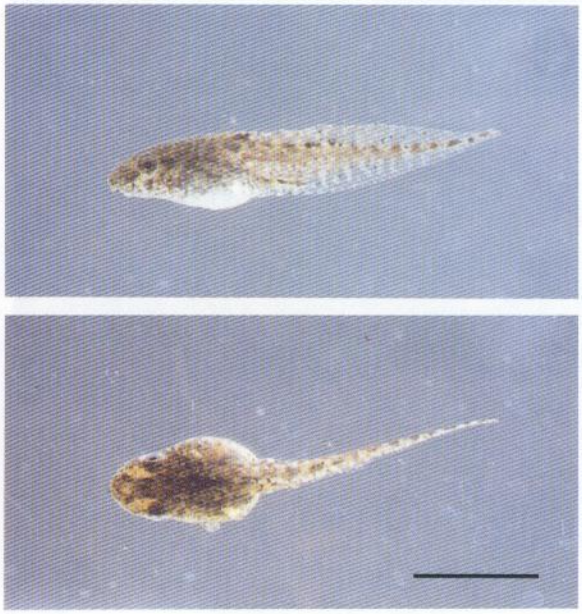

Figure 2. Lateral and dorsal views of larval *Rana taipehensis* from Kungputze. Scale line = 1cm.

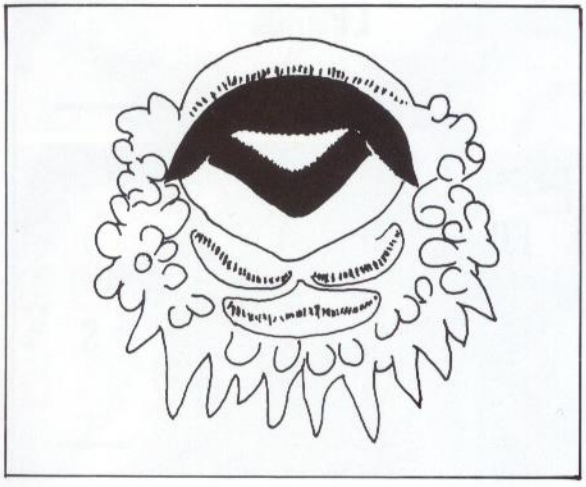

Figure 3. Oral disc of a larval *Rana taipehensis* [stage 31; upper jaw width = 1.6mm. The labial tooth row formula is 1/2(1)].

formula 1/2(1), length of the outermost lower labial tooth (P-2) almost equal to either side of the discontinuous row (P-1); jaw sheaths with black margins, finely serrated, upper with weak medial convexity. Spiracle sinistral, tube free at end; distance to snout 0.69-0.76 of head-body length. Vent tube dextral, attached to ventral fin. Tail lanceolate, both margins weakly convex tapering gradually to acute tip; tail length 1.59-1.99 of head-body length, maximum height 0.27-0.35 of tail length; caudal muscle deeper than either fin in proximal half of tail; origin of dorsal fin at end of body; height of dorsal fin equal to ventral. Lateral line not conspicuous. No glands visible.

In life head-body and tail greenish brown mottled with dark brown markings, iridophores and xanthophores present. Patches of dark markings in the dorsal, ventral and posterolateral surfaces of the tail muscle. Dark stripe extends vertically across the iris through the center of the pupil. Horizontal bars present anteriorly and posteriorly to the eyes. A dark mark under the eye occurs in some tadpoles.

Internal features.--Prelingual arena of floor triangular (Figure 4), bounded posteriorly by a flattened palp in each lateral corner; concave palps face forward, margins pustulose; a median low ridge with a large, rounded pustule anterior to the palps; a curved row of 4-5 pustules extending from the ridge to each corner of lower jaw. Tongue anlage wide, with 2 long, subequal lingual papillae. Buccal floor arena an elongate oval, poorly defined by a curved row of 9 single or basally fused papillae in each lateral border; papillae curve anteromedially, the posterior pair slightly further apart from the other; anterior one-third of interior smooth, with about 45 evenly scattered pustules in posterior two-third extending to base of ventral velum. Buccal pockets transverse, curved, closer to base of velum than to tongue anlage. One papilla and about 7 pustules anterior to buccal pocket and lateral to buccal floor arena on each side. Ventral velum continuous with delicate spicular support; margin wavy, with a median projection bounded by two low projections between the filter chambers and 3 short projections on each side; secretory pits present but largely limited to peaks on velar margin. Glottis largely exposed, lips distinct. Branchial baskets oblique, widely exposed behind velum, both baskets contact anterior to glottis; 3 gill chambers on each side; length of middle chamber about half the length of floor behind prelingual arena; filter mesh dense with tertiary and higher folds; filter rows of relatively uniform width, slightly separated; filter canals narrow.

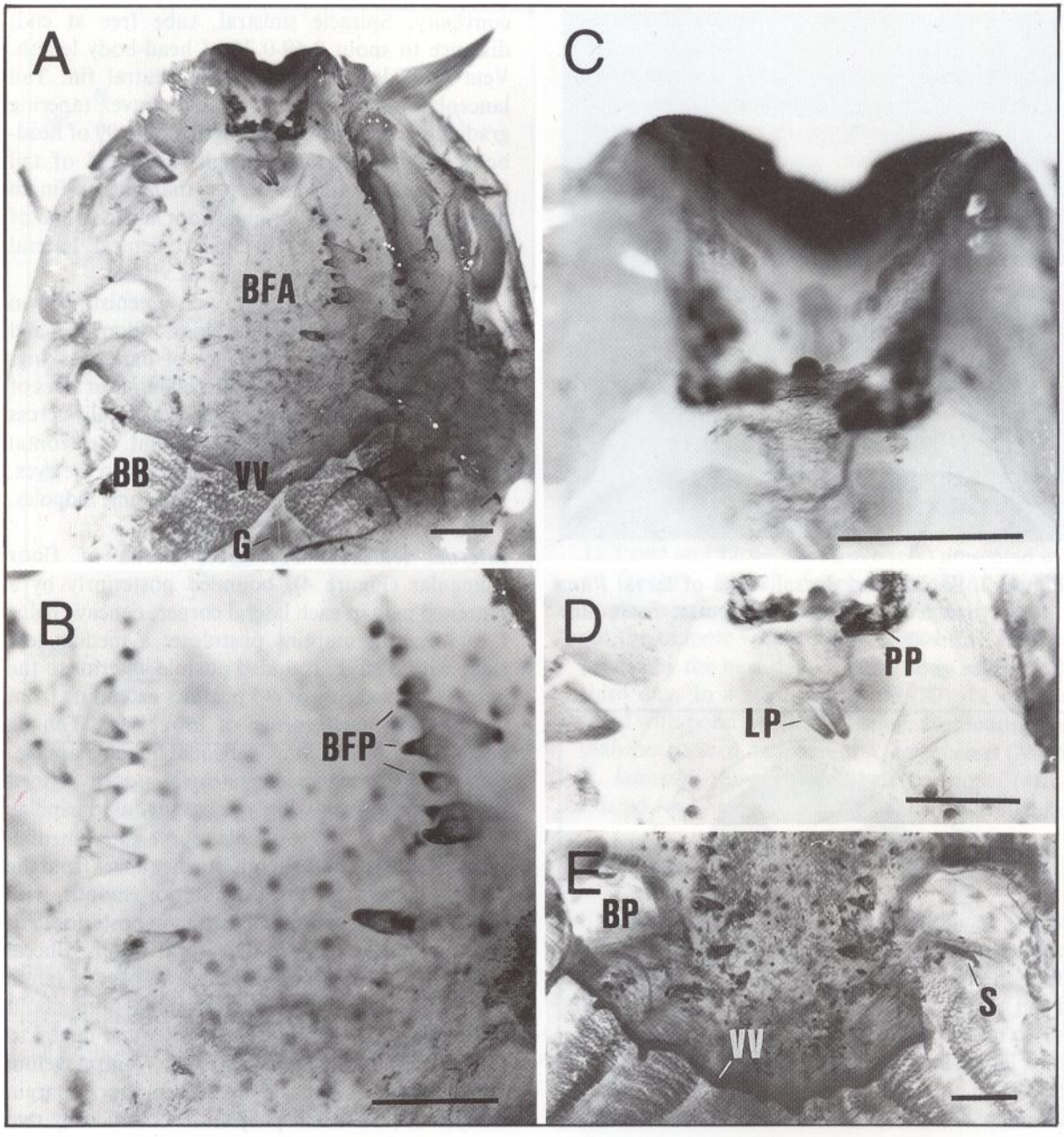

Figure 4. Floor of buccal cavity of larval *Rana taipehensis:* (A) Overview of the floor; (B) Buccal floor arena; (C) Prelingual arena, showing the median and rows of pustules on lateral walls; (D) Tongue anlage with two lingual papillae; (E) Ventral velum, partly cut away at right to show the spicule. BB = Branchial basket; BFA = Buccal floor arena; BFP = Buccal floor papillae; BP = Buccal pocket; G = Glottis; PP = Prelingual palp; S = Spicule; VV = Ventral velum. Scale line = 0.5mm.

Prenarial arena of roof hexagonal (Figure 5) with an M-shaped array of short pustules midway between the jaw sheath and choanae; the median pustule are rounded and larger than others.

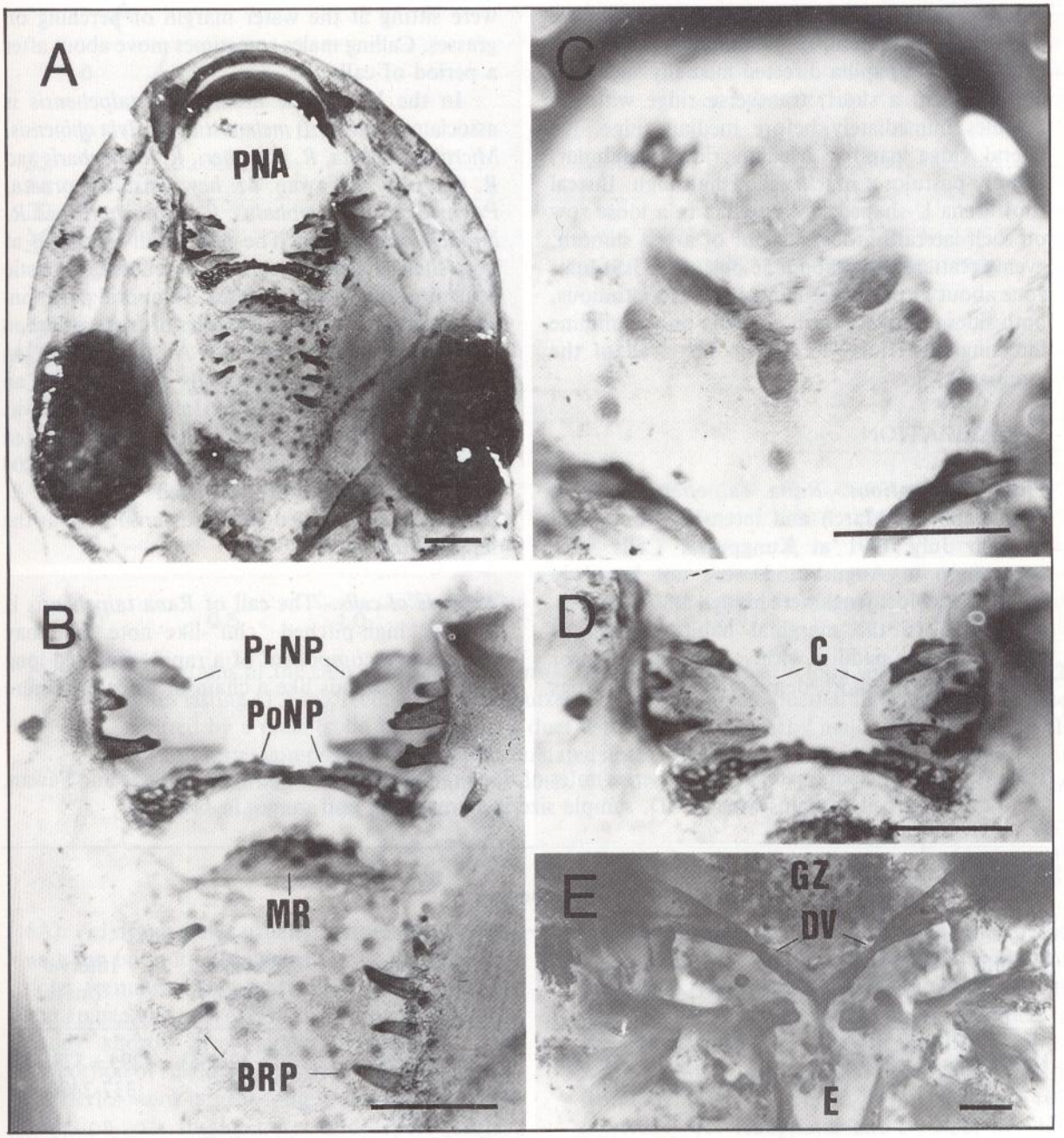

Figure 5. Roof of buccal cavity of *Rana taipehensis:* (A) Overview of the roof; (B) Postnarial arena and buccal roof arena with median ridge and lateral ridge papillae; (C) Prenarial arena showing pustules arrayed like an "M"; (D) Choanae with papillae; (E) Dorsal velum and esophagus. BRP = Buccal roof papillae; E = Esophagus; GZ = Glandular zone; MR = Median ridge; C = Choanae; PNA = Prenarial arena; PoNP = Postnarial papillae; PrNP = Prenarial papillae. Scale line = 0.5mm.

Choanae oval, widely separated; narial walls smooth, margin rimmed, pustulose anteriorly, raised posteriorly; a long, anteriorly pustulose papilla rising from lateral corner on each side of

anterior wall. Postnarial arena with 4-5 pustulose papillae posterolateral to postnarial wall on each side, one long papilla directed medially such that apices touch; a short, transverse ridge with 3-4 pustules immediately before median ridge. No lateral ridge papilla. Median ridge semilunar, densely pustulose; much wider than high. Buccal roof arena U-shaped; 3-4 papillae in a loose row on each lateral border; interior of arena smooth, evenly scattered with about 55 pustules. Glandular zone about 11 pits deep. Dorsal velum continuous, both sides obliquely form a funnel on the midline directing posteriorly to the knobby wall of the esophagus.

VOCALIZATION

Field observations.--*Rana taipehensis* called sporadically in March and intensely from April through July 1991 at Kungputze. Calls were uncommon in August and were not heard in September. Most frogs were hidden among grasses by ponds. In the marginal habitats, such as abandoned rice paddies with scanty vegetation or soggy fields with short, dense grasses, a few frogs were sitting at the water margin or perching on grasses. Calling males sometimes move about after a period of calls.

In the Kungputze area, *Rana taipehensis* is associated with *Bufo melanostictus, Hyla chinensis, Microhyla ornata, R. guentheri, R. limnocharis* and *R. tigerina*. At Fawan, *M. heymonsi, M. ornata, Polypedates megacephalus, R. limnocharis* and *R. latouchii* are present. The calls of all associates at both sites have interspecific differences in acoustic structures (unpublished data). Temporal partitioning in vocal activity of all species of frogs at Fawan involved two distinct periods. All the frogs began to call in dense grass by ponds near sunset at an air temperature of 27°C. Initial activity was sporadic, but shortly afterward all the associated species began calling and choruses lasted until 0200 when the temperature dropped to 24°C. *R. limnocharis* continued to chorus until 0530 at the temperature of 22°C.

Analysis of calls.--The call of *Rana taipehensis* is a faint, high-pitched "chu"-like note that may constitute a component of a rapid, repeated long series that sounds like a chain of whistles (Figure

Table 1. Acoustic parameters of short series notes of *Rana taipehensis* recorded at Kungputze and Fawan. Each cell contains Mean ± SD, sample size in parentheses and ranges in brackets.

Locality	Temp. (°C)	Call type*	Frequency: Fundamental (Hz)	Frequency: 2nd harmonic (Hz)	Duration (ms)	Interval (ms)
Kungputze	24	L	1967 ± 236 (85) [1500-2400]	3914 ± 386 (85) [3000-4840]	70 ± 12 (85) [37-93]	1299 ± 578 (45) [337-2400]
		H	1820 ± 148 (24) [1520-2160]	3562 ± 248 (24) [3120-4000]	108 ± 16 (24) [68-137]	673 ± 141 (12) [462-915]
Fawan	27	L	1979 ± 142 (69) [1680-2240]	3961 ± 278 (69) [3360-4480]	66 ± 10 (69) [43-87]	471 ± 134 (40) [310-943]
		H	1685 ± 204 (59) [1360-2240]	3367 ± 390 (59) [2800-4480]	67 ± 9 (59) [50-93]	442 ± 128 (57) [237-802]

* L = low-dominated note; H = high-dominated note. See text for definitions.

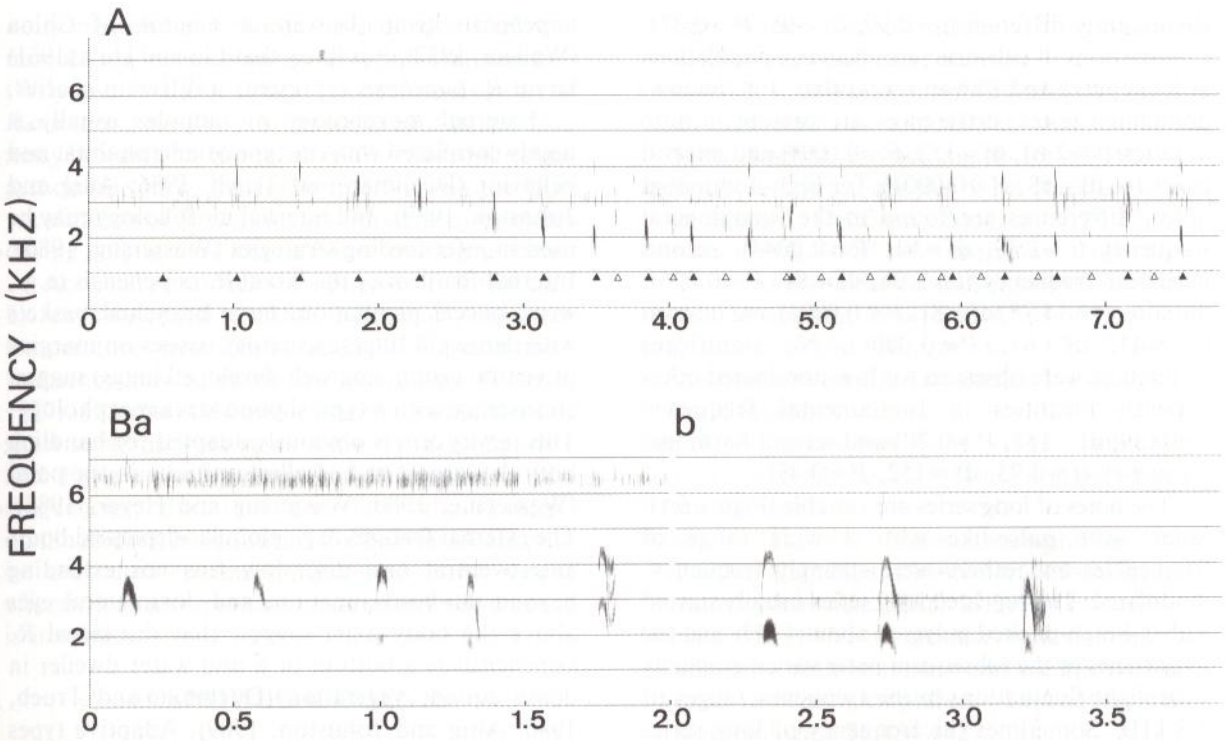

Figure 6. Sonograms of the calls of *Rana taipehensis*. (A) Anterior part of a long series that contains 25 notes lasting 11.5 sec, recorded at Kungputze (24°C), showing the fluctuating frequencies of notes emitted by a male (solid triangles) in a duet with notes of a nearby male (open triangles); (B) A short series composed of five high-dominated notes recorded at Kungputze, 24°C (a) and short series containing three low-dominated notes recorded at Fawan, 27°C (b). The transform size of the sonogram is 100 pts (300 Hz).

6A). Adjacent males usually form choruses. The note can be emitted singularly or in 2-5 successive notes forming a slow short series (Figure 6B). At Kungputze, the calls of a male in an abandoned rice paddy shortly after sunset included a large proportion of single notes or short series. Later, the call series were largely long series with sporadic emission of single note and short series. Occasionally, long series and short series would be emitted alternately.

The single note and notes of short series are well-tuned with rapid rise-times and strong frequency modulation. Sonograms of this sort of notes show a parabolic curve spanning a wide frequency range with multiple harmonics. High-dominated and low-dominated forms of this note are defined according to the positions of the dominant frequencies (Figure 6). The high-dominated note is strongest in the second harmonic whereas the low-dominated note is strongest in the first. All sampled individuals made both types of calls. Table 1 shows the acoustic parameters of short series notes recorded at Kungputze and Fawan. Significant differences are found between low and high-dominated forms in fundamental frequencies ($t = 2.89$, $df = 107$, $P = 0.0047$ for Kungputze and $t = 9.56$, $df = 126$, $P < 0.0001$ for Fawan), second harmonic frequencies ($t = 3.58$, $df = 107$, $P = 0.0005$ for Kungputze and $t = 10.01$, $df = 126$, $P < 0.0001$ for Fawan) and note intervals ($t = 3.85$, $df = 55$, $P = 0.0003$ for Kungputze). Differences in durations of notes between low and high-dominated notes are evident in the calls from Kungputze ($t = 12.85$, $df = 107$, $P < 0.0001$) but not from Fawan ($t = 0.75$, $df = 126$, $P = 0.45$). Note interval between low and high-dominated notes from Fawan was not

significantly different ($t = 0.90$, df = 95, $P = 0.37$). Comparisons of call structures between populations at Kungputze and Fawan reveal that, for the low-dominated notes, differences are present in note duration ($t = 2.61$, df = 152, $P = 0.0099$) and interval ($t = 9.16$, df = 83, $P < 0.0001$); for high-dominated notes, differences are found in the fundamental frequency ($t = 2.39$, df = 81, $P = 0.0044$), second harmonic frequency ($t = 2.26$, df = 81, $P = 0.026$), duration ($t = 14.75$, df = 81, $P < 0.0001$) and interval ($t = 5.43$, df = 67, $P < 0.0001$). No significant differences were observed for low-dominated notes between localities in fundamental frequency ($t = 0.39$, df = 152, $P = 0.70$) and second harmonic frequency ($t = 0.73$, df = 152, $P = 0.47$).

The notes of long series are variable (Figure 6A). Some were pulse-like with a wide range of frequencies and others were strongly frequency-modulated. The repeated long series usually started with 3-4 high-pitched pulses at about 4 kHz and the frequencies of the subsequent notes varied gradually with slight fluctuations in the frequency ranges of 2-3 kHz. Sometimes the frequency of long series notes dropped to 1.8 kHz. Intensity of each note in long series also varied. A long series sampled from an individual from Kungputze contained 25 notes lasting 11.5 sec. The mean duration and interval of this call series were 32 ± 6 ms (N = 25) and 414 ± 125 ms (N = 24) respectively, both significantly shorter than those of low-dominated call of short series ($t = 15.50$, df = 108, $P < 0.0001$ for durations and $t = 0.76$, df = 67, $P < 0.0001$ for intervals). Acoustic structure of long series from Kungputze and Fawan populations are similar.

DISCUSSION

Rana taipehensis and *R. macrodactyla* are closely related and occur sympatrically in many localities outside of Taiwan. Their larval morphologies are nearly identical (Pope, 1931; Wallace, 1937). Liu and Hu (1961) illustrated a larval *R. taipehensis* with similar oral structure, but its external features and pigmentation pattern were peculiar. This tadpole has a medial vent tube, gray head-body, thin and transparent ventral skin, darkly mottled fins and caudal muscle with homogeneous pigmentation. Although not mentioned in the text, dorsolateral folds clearly are present on the head-body in the illustration. These features are not found in the tadpole of *R. taipehensis* from Taiwan or Canton of China (Wallace, 1937). It is likely that Liu and Hu's (1961) larval *R. taipehesis* represents a different species.

External morphology of tadpoles usually is highly correlated with the type of microhabitat and behavior (Duellman and Trueb, 1986; Altig and Johnston, 1989), and internal morphology may be used to infer feeding strategies (Wassersug, 1980). Internal features of the larval *R. taipehensis* (e.g., weak buccal papillation, large branchial baskets with dense gill filters, secretory tissues on margins of ventral velum, and well-developed lungs) suggest consistence with a typical pond larva morphology. This larva form is obviously adapted for handling both the largest and smallest particles in the pond (Wassersug, 1980; Wassersug and Heyer, 1988). The external features (e.g., globular-depressed body, anteroventral oral disc, low fins not extending beyond tail-body junction, and dorsolateral eyes above the body axis) suggest that the larval *R. taipehensis* is a bottom or a mid-water dweller in dense aquatic vegetation (Duellman and Trueb, 1986; Altig and Johnston, 1989). Adaptive types inferred from the larval morphology are consistent with the microhabitat preference and foraging behavior observed in the field and laboratory. The broad spectrum of food sizes and types examined from larval *R. taipehensis* implies a dietary generalist. The tadpoles may either perform suspension-feeding among aquatic vegetation or graze on detritus at the bottom. Nevertheless, the large proportion of soil and vegetative fragments in the diet suggests that larval *R. taipehensis* be regarded as more of a detritus feeder than a microphagous suspension feeder.

Internal oral morphologies of tadpoles are distinctive at the generic level of leptodactyloid frogs (Wassersug and Heyer, 1988). The three larval forms of the subgenus *Hylarana* from Borneo are diagnosed by three features not found in other Bornean ranids: (1) wide and curved flaps located posterolaterally to the prelingual arena; (2) a transverse row of pustules present immediately in front of the median ridge; and (3) absence of the lateral ridge papilla or flap (Inger, 1985). All the tadpoles in this group from Taiwan (e.g., *adenopleura, guentheri, latouchii, swinhoana* and *taipehensis;* see Frost, 1985) also have these features (unpublished data).

Acoustic features of anurans allow species recognition and modify behavioral responses. In

noisy environments, vocal features with frequency modulation tend to enhance sound transmission (Wily and Richard, 1982). The whistle-like call of *Rana taipehensis* is postulated to be adapted to a noisy breeding habitat in which the calls of the eight associated species inevitably interfer with the faint vocalization of *R. taipehensis*. Movement by males during calling may also enhance mating success.

Acoustic parameters are intensively influenced by environmental factors, particularly ambient temperature (Kuramoto, 1987). The dominant frequency may correlate the body weight (Veloso, 1977). Comparisons of the acoustic parameters of short series between populations from Kungputze and Fawa reveal remarkable differences in the frequencies, durations and intervals of high-dominated notes. However, these differences could be attributed to temperature and body weight effects; it is also probable that genetic divergence is involved.

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臺北赤蛙(*Rana taipehensis*)的蝌蚪與鳴聲

周文豪

摘 要

臺北赤蛙的蝌蚪外型及口腔內部結構顯示其爲典型的池沼型蝌蚪。牠們能在池底或中層的水生植叢中生活，覓食各種不同大小的食物，其中包含大量的泥質與腐質。雄蛙的鳴聲是一種微弱、似口哨的單音。此單音可在合鳴時快速重複組成長鳴；少數幾個單音亦可緩慢重複組成短鳴。相隔兩長鳴之間往往出現單音或短鳴，兩者的基頻範圍分別爲1.8－4.0kHz和1.3－2.4kHz。本文亦澄清本種蝌蚪形態誤載，同時也比較兩相隔離族群的鳴聲。

關鍵詞：蝌蚪、鳴聲、臺北赤蛙、赤蛙科、無尾目。