Journal of Zoology. Print ISSN 0952-8369

Temporal organization of an anuran acoustic community in a Taiwanese subtropical forest

M.-Y. Hsu[1], Y.-C. Kam[2] & G. M. Fellers[3]

1 Department of Biology, National Changhua University of Education, Changhua, Taiwan
2 Department of Life Science, Tunghai University, Taichung, Taiwan
3 Western Ecological Research Center, USGS, Point Reyes National Seashore, Point Reyes, CA, USA

Keywords
acoustic community; amphibian; subtropical anuran.

Correspondence
Yeong-Choy Kam, Department of Life Science, Tunghai University, Taichung 407, Taiwan.
Email: biyckam@thu.edu.tw

Received 22 June 2004; accepted 14 September 2005

doi:10.1111/j.1469-7998.2006.00044.x

Abstract

We recorded anuran vocalizations in each of four habitats at Lien Hua Chih Field Station, Taiwan, between July 2000 and July 2001. For each 27 biweekly sample, eight recorders taped calls for 1 min out of every 11 between the hours of 17:00 and 07:00. We obtained 11 481 recordings with calls, and identified 21 503 frogs or groups of frogs. These included 20 species, with an average of 10.4 ± 3.5 species calling each night. Some species called year round, others called in the spring and summer, and a third group called only in the fall and winter. The number of species calling and the maximum calling intensity were correlated with both rainfall and air temperature. The nightly pattern of calling varied among species. Most species called continuously throughout the night, whereas some had a peak right after dusk. A few species had different nightly calling patterns in different habitats. Both *Rana limnocharis* and *Rana kuhlii* changed their calling pattern in the presence of large choruses of other anuran species.

Introduction

During the breeding season, many species of frogs form aggregations and call to attract potential mates. Acoustic environments can be very complex in such choruses, with many species calling at the same time (Duellman & Pyles, 1983; Garcia-Rutledge & Narins, 2001). In such environments, it is important for female frogs to recognize the calls of conspecifics in order to select proper mates. For males, calling is energetically expensive (Pough *et al.*, 1992; Runkle *et al.*, 1994), and hence males of different species use various temporal or spatial calling strategies to communicate more efficiently with conspecifics (Wells, 1977; Duellman & Trueb, 1986; Sullivan, Ryan & Verrell, 1993; Garcia-Rutledge & Narins, 2001).

Anuran acoustic interactions have been the subject of many observational and experimental studies designed to elucidate anuran communications and interactions (Wells, 1977; Fellers, 1979; Schwartz & Wells, 1984, 1985; Howard & Palmer, 1995; Bevier, 1997). Other workers have used frog choruses to monitor populations in various parts of the world (Heyer *et al.*, 1994; Parris, Norton & Cunningham, 1999; Corn, Muth & Iko, 2000). However, in tropical and subtropical regions with high diversity, basic information about anuran acoustic communities has not been well reported or studied (Bridges & Dorcas, 2000; Garcia-Rutledge & Narins, 2001), perhaps because this type of work is both time consuming and tedious. Thus, the development of automated recording systems provides an opportunity to study the acoustic assemblages of anurans more efficiently (Heyer *et al.*, 1994; Bridges & Dorcas, 2000). An automated recorder has the advantage of allowing researchers to collect data on calling anurans for an extended period without disturbing the frogs, and it can be used in habitats that are difficult or dangerous to access at night. Parris *et al.* (1999) and Hsu, Kam & Fellers (2005) reported that automated recorders detected 71 and 91% of the species that inhabit study areas in south-east Queensland (Australia) and central Taiwan, respectively.

Amphibians' activity is principally regulated by temperature and moisture (Duellman & Trueb, 1986; Rome, Steven & John-Alder, 1992), and activity levels reflect the physiological condition of organisms (Licht, 1969; Wiest, 1982; Pough *et al.*, 1983). It is generally believed that tropical and subtropical species are capable of reproduction throughout the year, and that activity is primarily controlled by the rainfall. Frogs may call year round, but only breed in restricted parts of the wet season. In contrast, temperate species are typically seasonal breeders, and activity is mainly controlled by temperature and/or rainfall (Duellman & Trueb, 1986). Recent studies, however, demonstrate that the reproductive activity of subtropical frogs is governed by temperature rather than rainfall (Kam & Chen, 2000; Chen, Kam & Lin, 2001).

Amphibians on Taiwan dispersed from mainland tropical and temperate regions of Asia to the island via land bridges during Pleistocene periods of lower sea level (Zhao, 1999). The assemblage of species that became established on

Taiwan is unique, with a combination of endemic species (22%) and species shared with the adjacent mainland (Lue, Tu & Shang, 1999; Zhao, 1999).

The purpose of our study was to describe the temporal structure of the anuran acoustic assemblage in a Taiwanese subtropical lowland forest at Lien Hua Chih, inhabited by at least 22 anuran species (Hsu *et al*., 2005). We evaluated the (1) composition of the acoustic assemblage throughout the year, (2) annual calling pattern for each species, (3) nightly calling pattern and (4) correlation between the acoustic activity and weather.

Methods

Study area

Field work was conducted from July 2000 to July 2001, at the Taiwan Forestry Research Institute experimental forest at Lien Hua Chih Field Station (23°55′N, 120°52′E), Nantou County, in central Taiwan. The station encompasses a 461-ha watershed: half is covered by undisturbed lowland primary forest, and the rest is covered by artificial plantations and agricultural farmlands. The site is characterized by low topography, with elevations ranging from 576 to 975 m. The mean annual air temperature is 21.1 °C, and ranges from 9.9 °C in January to 30.0 °C in July. The area receives *c*. 220 cm of rain annually. Although it rains in all months, the wet season begins in May and ends in August (Fig. 1). Heavy rains are most often associated with the ‘plum rains’ or ‘Mei rains’ in the spring (April–June) and the typhoon season in the summer (July–September). The ‘plum rain’ season is characterized by continuous light rain for many days, with occasional heavy thunderstorms. Typhoons usually bring heavy rains that can cause flash floods and damage to the forests.

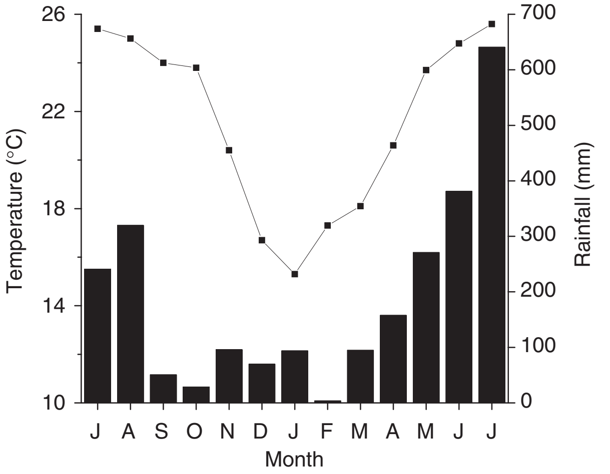

Figure 1 Monthly mean air temperature (line) and precipitation (bars) at Lien Hua Chih, Taiwan. The data are from July 2000 to July 2001.

Survey sites

We established study sites in four habitats: a temporary pond, a permanent pond, an ephemeral stream and a permanent marsh. The temporary pond was filled with water in the spring and summer (March–September), but was dry in the fall and winter (October–February). The pond was surrounded by elephant grass *Pennisetum purpureum* and bamboo stands *Phyllostachys* sp. It covered *c*. 400 m^2 during the wet season. The permanent pond was a 450 m^2 abandoned paddy field that held water all year, even though the water level dropped during the dry season. The ephemeral stream included both riffles and pools, and was 1–3 m wide and 20–30 cm deep during the wet season. During the dry season, the flow was reduced, resulting in the formation of intermittent pools. Stream channels were lined with cobblestones, bedrock and boulders. The stream was completely shaded by broadleaf trees (*Michelia formosana*, *Adenanthera microsperma*, *Pellionia radicans*, *Entada phaseoloides*). The shallow, permanent marsh was 25 m^2 in area and fed by a spring. The dominant vegetation was *Juncus effuses*, *Cynodon dactylon* and *Dicranopteris linearis*. The marsh was located at the edge of a primary forest consisting of *Mich. formosana*, *Gordonia axillaries*, *Cyathea metteniana* and *Prunus campanulata*.

Sampling techniques

We surveyed biweekly for frogs using an automated recording system. The system consisted of an AIWA (Taiwan) TP-VS480 tape recorder (with AE-120 TDK tapes), a 12 V rechargeable battery, a timer (CEC, Type-CTW) housed in a waterproof box and an AIWA external stereo-microphone. The microphone was secured to a tree *c*. 2 m above the ground. Each recorder began taping at 19:00 h, recorded for 1 min and then turned off for 11 min. This cycle was repeated until 07:00 h the next morning. In theory, we could obtain 60 min of recording each night, but we only recorded 57–58 min because of a slight delay in starting the recorder.

We placed two recorders at each site, 50 m apart. The results from the two recorders were pooled for each night. Recordings were played back in the laboratory, and we identified each vocalization to species. The results for *Microhyla heymonsi* and *Microhyla ornata* were combined because it was difficult to distinguish their calls reliably. We assumed that most calls were *Micr*. *heymonsi*, because our line-transect sampling in an earlier study (Hsu *et al*., 2005) revealed that *Micr*. *heymonsi* outnumbered *Micr*. *ornata* by 973 to 3. Because of the scarcity of calls, we did not analyze our data for *Bufo bankorensis*, *Bufo melanostictus*, *Hyla chinensis*, *Buergeria japonica* and *Rana rugulosa*.

The day before and after each nocturnal recording session, we surveyed the pond, marsh or stream and recorded the number of amplexing pairs, egg clutches and/or tadpoles in order to evaluate the reproductive activity for each species. We found that *Rana adenopleura* tadpoles overwinter, so we used the presence of amplexing pairs and egg clutches as evidence of reproduction for that species.

Egg clutches and tadpoles were identified to species using oviposition site, morphological structures of the body and oral discs (Chou & Lin, 1997; Lue *et al*., 1999).

Data analyses

Anuran calling intensity was quantified according to a modified version of the classification scheme used by Bridges & Dorcas (2000), as recommended by the North American Amphibian Monitoring Program (US Geological Survey, http://www.pwrc.usgs.gov/naamp/). Calling intensity was scored as follows: 0, no calling recorded; 1, only one male heard calling; 2, multiple males calling, but not a full chorus; 3, many males calling in a full chorus.

We conducted 27 surveys, and set up eight recorders, two for each site, for each survey. If all recorders successfully detect frogs in all 27 survey nights, we would have 1080 sampling points for each hour (i.e. 5 sampling points/recorder · h × 8 recorders/survey night × 27 survey nights). We treated each 1-min recording as one data point. The maximum calling intensity from 0 to 3 for each species was determined for each data point.

Maximum calling intensity was defined as the highest level of calling intensity for each species from any site on a given night. For example, the highest calling intensity of *Ra. adenopleura* on 14 October 2000 at the four sites (the temporary pond, permanent pond, ephemeral stream and permanent marsh) was 2, 3, 1 and 1. We used intensity level 3 as the maximum calling intensity for this species on that night. *Cumulative maximum calling intensity* was defined as the sum of the maximum calling intensities of all species for each sampling night. For example, there were five species calling on 14 October 2000, and the maximum calling intensity of each species was 2, 3, 1, 1 and 2. The cumulative maximum calling intensity for that night was 9. The *mean calling intensity* was defined as the mean of maximum calling intensity for each 12-min period in each hour. This was calculated for each species.

In each of the four habitats, we used Hobo data loggers (Onset Computer Corp., Bourne, MA, USA; www.onsetcomp.com) to record relative humidity and average, maximum and minimum temperature each night. Air temperature 4 days pre-survey was the mean air temperature during the 4 days before recording. Rainfall data were obtained from a local weather station located within 1.7 km of all sampling sites. We calculated the total rainfall 24 and 96 h before each sampling night. These weather variables, i.e. air temperature and rainfall 4 days before survey, were designated as latent variables of environments that potentially affect the frog calling.

We used the Pearson correlation coefficients to assess correlations between calling and weather. Data for all four sites were combined to give the total number of species detected on each survey night (i.e. the cumulative number of species of calling frogs) and these data were log-transformed to meet the parametric assumption of normality. A stepwise regression was used to determine the relative importance of weather variables in predicting maximum calling intensity for each species. We performed statistical analyses using SAS (SAS Institute Inc., 1996), and used a *P*-value of 0.05 to evaluate statistical significance.

Results

Twenty-seven biweekly surveys were conducted at each of the four sites from July 2000 to July 2001 (Table 1). We obtained recordings from 11 481 1-min sampling periods, and identified 21 503 frogs or groups of frogs. Twenty species were recorded, with an average of 10.4 ± 3.5 (range 1–12) species per night. Our equipment failure rate was low, only 6% (13/216).

Chirixalus eiffingeri, *Chirixalus idiooctocus*, *Rhacophorus moltrechti*, *Rhacophorus taipeianus*, *Microhyla* sp., *Ra. adenopleura, Rana Kuhlii and Rana latouchi* occurred in all four habitats (Table 1). *Chirixalus eiffingeri, Ra. adenopleura, Ra. latouchi and Rana swinhoana* were detected during every survey (Table 1). The number of species calling varied seasonally; more species called in the spring and summer, whereas fewer species called in the fall and winter (Fig. 2a). A similar pattern was seen in the number of species breeding (Fig. 2b). There was a significant correlation between the number of species calling and the number of species with evidence of breeding ($r = 0.94$, $P < 0.0001$).

The calling pattern for each species fits one of three categories. Continuous callers were recorded year round, even though calling intensity varied seasonally (*C. eiffingeri*, *Ra. adenopleura*, *Ra. latouchi* and *Ra. swinhoana*; Table 2). Spring–summer callers called throughout the spring and summer, with either no calling during the fall or winter (*Polypedates megacephalus*, *Microhyla* sp., *Rana guentheri*, *Rana limnocharis* and *Rana psaltes*) or only low-intensity calls during that time of year (*C. idiootocus*, *Buergeria robustus* and *Ra. kuhlii*). The calling period ranged from 6 to 9 months. Fall–winter callers called primarily in the fall and winter, and had a period with no calling during either the spring or summer. Even within this category, *Rh. taipeianus* and *Rana sauteri* had largely separate calling periods. *Rana sauteri* called from late summer to fall (September–December), whereas *Rh. taipeianus* called from fall to winter (October–April) and peaked in the winter. In contrast, *Rh. moltrechti* had less distinct calling and non-calling periods. This species called throughout all months of the year except October, and there was a slight increase in calling in the winter and spring (December–April).

A stepwise regression of the number of calling species with seven weather variables revealed that calling was significantly influenced only by total rainfall 4 days before survey (partial $r^2 = 0.39$, $P < 0.001$). In contrast, the cumulative maximal calling intensity of all species was influenced not only by the total rainfall 4 days before survey (partial $r^2 = 0.49$, $P < 0.001$) but also by the relative humidity (partial $r^2 = 0.09$, $P < 0.05$).

Stepwise regression of maximum calling intensity of each species with seven weather variables revealed that calling activity was influenced by temperature, humidity and rain (Table 3). For 10 species of frogs, rain during the 4 days

Table 1 Frequency of 20 anuran species recorded during 27 surveys using automated recorders in four habitats at the Lien Hua Chih field station, Taiwan

Species	Breeding habits	Temporary pond	Permanent pond	Ephemeral stream	Permanent marsh	All habitats combined
Bufonidae						
Bufo bankorensis	F–W; aggregation; aquatic eggs and tadpoles; lotic	–	–	1	–	1
Bufo melanostictus	S–S; aggregation; aquatic eggs and tadpoles; lentic	1	–	–	1	2
Hylidae						
Hyla chinensis	S–S; aggregation; foam nest on land; aquatic tadpoles; lentic	1	1	–	–	2
Rhacophoridae						
Buergeria japonica	S–S; aquatic eggs and tadpoles; lotic	–	–	1	2	3
Buergeria robustus	S–S; aggregation; aquatic eggs and tadpoles; lotic	11	4	4	–	12
Chirixalus eiffingeri	S–S; arboreal eggs (tree holes); aquatic oophagous tadpoles	9	16	25	24	27
Chirixalus idiootocus	S–S; aggregation; terrestrial eggs; aquatic tadpoles; lotic	19	15	5	18	22
Polypedates megacephalus	S–S; aggregation; foam nest on land; aquatic tadpoles; lentic	15	15	–	3	15
Rhacophorus moltrechti	F–W; foam nest on land, aquatic tadpoles; lentic	3	2	8	20	20
Rhacophorus taipeianus	F–W; aggregation; foam nest on land, aquatic tadpoles; lentic	10	11	8	11	12
Microhylidae						
Microhyla sp.[a]	S–S; aggregation; aquatic eggs and tadpoles; lentic	13	14	5	13	14
Ranidae						
Rana adenopleura	S–S; aggregation; aquatic eggs and tadpoles; lentic	20	26	20	24	27
Rana guentheri	S–S; aquatic eggs and tadpoles; lentic	10	1	–	–	11
Rana kuhlii	S–S; aquatic eggs and tadpoles; lotic;	2	8	12	17	18
Rana latouchi	Year round; aquatic eggs and tadpoles; lentic and lotic	18	21	20	16	27
Rana limnocharis	S–S; aquatic eggs and tadpoles; lentic	8	6	–	10	13
Rana psaltes	S–S; aquatic eggs and tadpoles; lentic	–	1	–	13	13
Rana regulosa	S–S; aquatic eggs and tadpoles; lentic	6	6	–	–	9
Rana sauteri	F–W; aggregation; aquatic eggs and tadpoles; lotic	–	–	5	–	5
Rana swinhoana	F–W; aquatic eggs and tadpoles; lotic	–	–	27	18	27
Number of calling species		15	15	13	14	20
Maximum number of species calling simultaneously		10	9	8	12	

F–W, fall and winter breeders; S–S, spring and summer breeders.

[a] We could not differentiate the calls of *Micr. heymonsi* and *Micr. ornata*. See Methods.

pre-survey was the most important factor influencing calling intensity. In contrast, the calling intensity of *P. megacephalus*, *Rh. moltrechti*, *Rh. taipeianus* and *Ra. psaltes* was correlated with the mean air temperature 4 days pre-survey (Table 3).

The calling pattern varied among species on a nightly basis. The pattern for all species, except *Ra. kuhlii* and *Ra. limnocharis*, was similar among habitats, and hence data from all habitats were pooled. For some species (e.g. *P. megacephalus*, *Microhyla* sp. and *Ra. psaltes*), peak calling intensity occurred right after dusk, with a linear decrease until dawn (Fig. 3a). In contrast, *Ra. latouchi* was the only species that increased calling intensity through the evening with a peak after midnight (Fig. 3b). The remaining eight species called throughout the night at a fairly constant level (Fig. 3c).

The nightly pattern of two frogs (*Ra. kuhlii* and *Ra. limnocharis*) differed among habitats (Fig. 4a and b). *Rana kuhlii* at the permanent pond called predominantly after midnight. In contrast, frogs in the permanent marsh

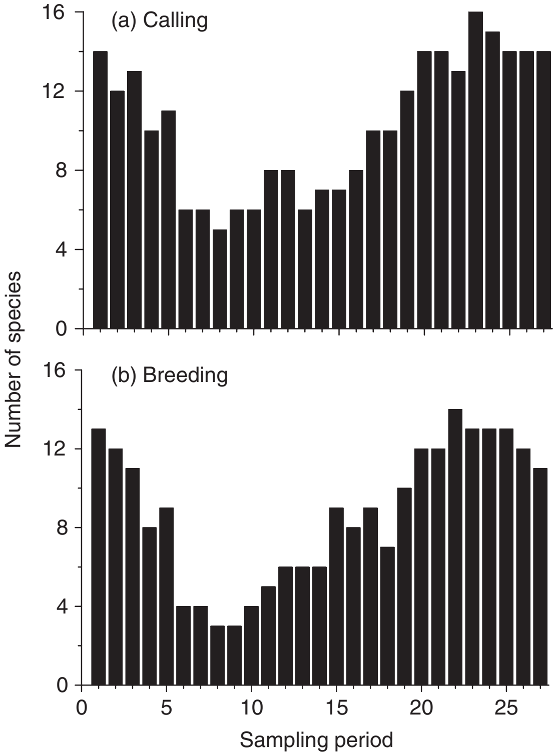

Figure 2 (a) Number of calling and (b) breeding species during each of 27 sampling periods. Most surveys occurred at 14-day intervals; occasionally, the interval was shifted by 1 (n=7) or 2 (n=3) days. The first survey took place on 5 July 2000 and the last on 7 July 2001. The number of surveys corresponds to the following dates: 1=2000/7/5; 2=7/19; 3=8/2; 4=8/16; 5=8/31; 6=9/15; 7=9/30; 8=10/14; 9=10/28; 10=11/11; 11=11/25; 12=12/9;13=12/21; 14=2001/1/7; 15=1/19;16=2/1; 17=2/17; 18=3/3; 19=3/17; 20=3/31; 21=4/14; 22=4/28; 23=5/12; 24=5/26; 25=6/9; 26=6/23; 27=2001/7/7.

and ephemeral stream called throughout the night with varying levels of intensity (Fig. 4a). *Rana limnocharis* at the permanent pond called predominantly before midnight, whereas at the temporary pond they called predominantly after midnight. *Rana limnocharis* at the permanent marsh called with a low intensity throughout the night (Fig. 4b).

Discussion

During a 13-month period, we recorded 20 species of frogs and toads in the Lien Hua Chih area of central Taiwan. We know from previous work (Hsu *et al.*, 2005) and incidental observations that an additional species is present in the area (*Rana plancyi*). *Rana plancyi* was an abundant frog at our study site, but the lack of recordings is not surprising as this species has only a weak call.

The 21 species at Lien Hua Chih represent an unusually high diversity of anurans. No other sites in Taiwan, including Fushan, Huisun, Nanjenshan and others, have as many species as in Lien Hua Chih (P. C. Hou & K. Y. Lue, pers. comm.). This richness may be because Lien Hua Chih has a wide range of habitats that include both extensive wetlands and one of the few undisturbed lowland primary forests within the Puli basin. The wetlands have both permanent and temporary bodies of water, and include naturally occurring streams, ponds and marshes, as well as man-made habitats such as rice fields, bamboo groves and small irrigation reservoirs. This combination of natural and man-made habitats has allowed for a remarkably diverse anuran fauna.

Previous studies have shown that population size affects calling intensity (Mohr & Dorcas, 1999). At Lien Hua Chih, *C. idiootocus*, *Microhyla* sp. and *Ra. adenopleura* were the predominant species calling; their loud calls dominate the acoustic environment in the permanent marsh, and both temporary and permanent ponds.

A stepwise regression showed that the rain during the 4 days pre-survey was the most important factor influencing the calling activity of most spring–summer callers. During the early spring (March and April), the temperature is generally warm enough for most species to breed; however, rain is rather unpredictable and can vary dramatically depending on the movement of weather fronts. Hence, continuous rain for several days may be a prerequisite that triggers breeding activity early in the season before the more reliable rainy season begins in May.

During the fall and winter, there was little rain, except during occasional monsoon events; consequently, water levels in all habitats were low. Only six to nine species called during this time (mostly at a low calling intensity), so the acoustic environment was comparatively simple with little temporal overlap in calls. For *Rh. moltrechti* and *Rh. taipeianus*, calling activity was correlated more with temperature than rain. It seems that low temperature (*c.* 12–15 °C) stimulates the breeding activity of these winter breeders. For the stream breeders like *Ra. sauteri*, calling activity was inversely correlated with rain. As rain increases stream flow, the lack of rain results in conditions that are more favorable for breeding and the survival of both eggs and tadpoles. This is true for many tropical stream-dwelling species, such as *Hyla boans* (Aichinger, 1987), *Bufo marinus* (Zug & Zug, 1979; Aichinger, 1987), *Bufo regularis* (Menzies, 1963) and *B. melanostictus* (Jorgensen, Shakuntala & Vijayakumar, 1986).

Lien Hua Chih has a subtropical climate characterized by warm, wet summers and cool, dry winters. The climate allows anurans to breed all year, although most species restrict their activity to just one or two seasons. Calling activity was strongly related to temperature, relative humidity and rain. For seasonally breeding species, calling was always closely associated with amplexing pairs, eggs and tadpoles. During the spring and summer, most of the lowland habitats were filled with water, and many species initiated breeding. At this time, calling reached its peak with a great deal of temporal overlap both within and between species in all four habitats.

For those species that called year round, reproductive activity was not always closely associated with calling activity. For example, *Ra. swinhoana*, a riparian species, breeds only in the fall and winter (Kam *et al.*, 1998). In

Table 2 Maximum calling intensity of 15 anuran species from July 2000 to July 2001 at Lien Hua Chih field station, Taiwan

Species	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June	July
Spring–summer callers													
Buergeria robustus	2	2	0	0	0	0	0	1	2	0	1	1	1
Chirixalus idiootocus	2	2	2	0	0	0	2	2	2	3	3	2	3
Polypedates megacephalus	2	2	0	0	0	0	0	0	2	2	2	2	2
Microhyla sp.	3	3	0	0	0	0	0	0	2	3	3	3	3
Rana guentheri	2	1	0	0	0	0	0	0	1	1	2	2	2
Rana kuhlii	2	2	0	0	1	1	0	1	2	2	2	2	2
Rana limnocharis	3	2	0	0	0	0	0	0	3	2	2	2	2
Rana psaltes	2	2	0	0	0	0	0	0	1	2	2	1	2
Fall–winter callers													
Rhacophorus moltrechti	0	1	1	0	1	2	2	2	2	2	1	1	1
Rhacophorus taipeianus	0	0	0	1	1	2	2	2	2	2	0	0	0
Rana sauteri	0	0	1	1	1	1	0	0	0	0	0	0	0
Continuous callers													
Chirixalus eiffingeri	1	1	1	1	1	2	1	1	1	1	2	1	1
Rana adenopleura	3	3	2	1	1	1	1	2	2	3	3	2	3
Rana latouchi	2	2	2	1	2	2	1	2	2	2	2	2	1
Rana swinhoana	2	2	1	1	1	2	2	2	2	2	2	2	1
Total number of species calling	12	13	7	6	8	8	7	9	14	13	13	13	13

Calling intensity was categorized as follows: 0, no calling recorded; 1, only one male calling; 2, multiple males calling, but not a full chorus; 3, many males calling in a full chorus.

Table 3 Stepwise regression of maximum calling intensity and weather for 15 species of anurans in Lien Hua Chih, Taiwan

Species	Ambient temperature	Maximum temperature	Minimum temperature	Ambient temperature 4 days pre-survey	Relative humidity	Rain 4 days pre-survey
Rhacophoridae						
Buergeria robustus						0.36***
Chirixalus eiffingeri					0.17*	
Chirixalus idiootocus					0.1	0.19*
Polypedates megacephalus	0.31**					0.13*
Rhacophorus moltrechti				0.6***		
Rhacophorus taipeianus	0.06*			0.77***	0.03	
Microhylidae						
Microhyla sp.	0.19*		0.03			0.51***
Ranidae						
Rana adenopleura	0.15*					0.40***
Rana guentheri		0.15*				0.33**
Rana kuhlii		0.06				0.42***
Rana latouchi					0.08	0.14*
Rana limnocharis					0.13*	0.28**
Rana psaltes	0.4***				0.04	0.18*
Rana sauteri						0.15*
Rana swinhoana				0.04	0.07*	0.6***

Partial r^2 was calculated.

*,** and ***significant differences at the 0.05, 0.01 and 0.001 levels, respectively.

tropical areas, many anurans are opportunistic and breed whenever sufficient water is available (Crump, 1974; Duellman & Trueb, 1986). In Taiwan, this appears to be the case for *C. eiffingeri*, an arboreal frog that breeds in tree holes or bamboo stumps that receive water primarily from rain. In the montane areas of Chitou, in western Taiwan, this species breeds only during the wet season (spring and summer) (Kam, Chuang & Yen, 1996). In eastern Taiwan, however, there is abundant rain from seasonal monsoons, and *C. eiffingeri* has an extended breeding season that also includes the fall and winter (Yang Yi-Ru, pers. comm.). Hence, *C. eiffingeri* is an opportunistic species that breeds whenever water is available in tree holes and bamboo stumps. The year-round calling pattern suggests that these frogs maintain territories throughout much of the year in order to have a suitable site for breeding when it rains.

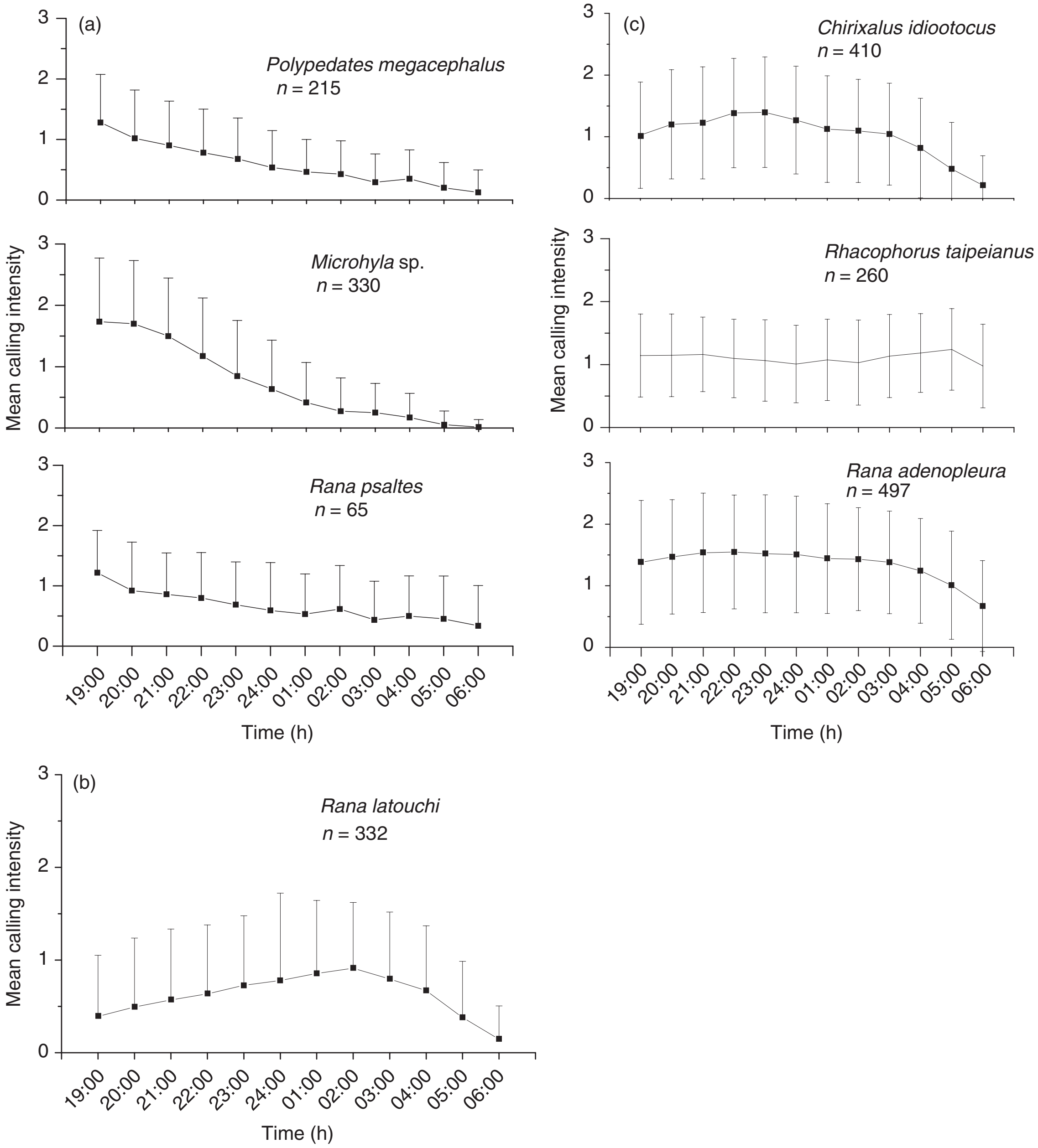

Figure 3 Calling patterns of anuran species with (a) decreased, (b) increasing and (c) stable calling intensity over the night. The mean (±SD) calling intensity was calculated by using calling intensity for all sampling points. A sampling point is a 1-min recording every 11 min (five samples per hour). See Methods for more details.

Interspecific differences in nightly calling activity were observed at Lien Hua Chih. Such differences have been reported in only a few other studies. Bridges & Dorcas (2000) and Mohr & Dorcas (1999) described the calling patterns of frogs in South Carolina, USA, and noted that many species showed distinct peaks either before or after midnight. In our study, most species called at a nearly constant rate for most of the night. Three species (*P. megacephalus*, *Microhyla* sp. and *Ra. psaltes*) showed a gradual decline in calling activity through the night (Fig. 3a), and two species (*Ra. kuhlii* and *Ra. limnocharis*) had different patterns in different habitats (Fig. 4).

Interspecific differences in calling patterns can be attributed to physiological, behavioral or phylogenetic differences between species (Bridges & Dorcas, 2000). Different patterns of calling may reduce competition for acoustic resources (Mohr & Dorcas, 1999; Garcia-Rutledge & Narins, 2001). We found that many species in our study area called at a constant intensity throughout the night, suggesting that acoustic resources may be partitioned spectrally or spatially,

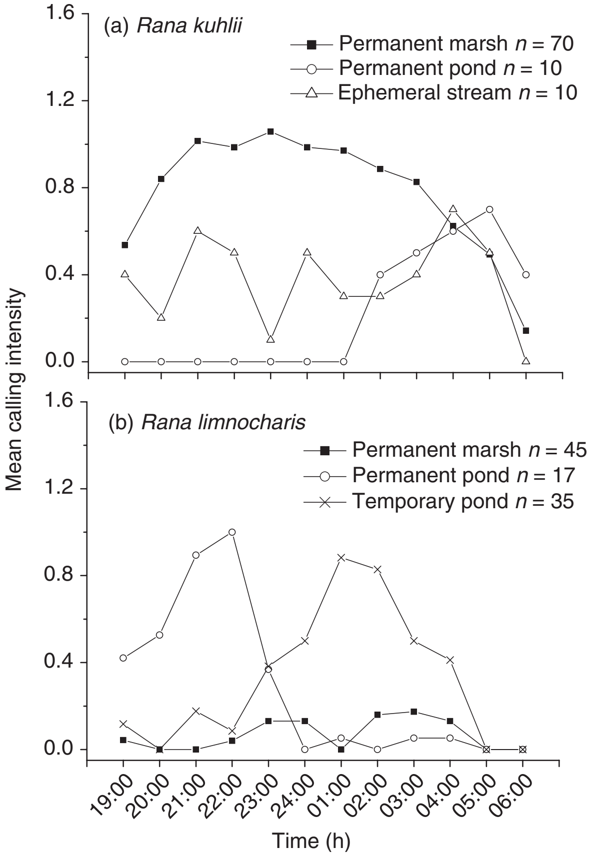

Figure 4 Calling patterns of (a) *Rana kuhlii* and (b) *Rana limnocharis* at three recording sites at Lien Hua Chih, Taiwan. The mean calling intensity was calculated by averaging the calling intensity of all sampling points. Each sampling point is a 1-min recording every 11 min (five per hour). See Methods for more details.

as occurs in other noisy, complex tropical environments (Duellman & Pyles, 1983; Garcia-Rutledge & Narins, 2001). Also, air temperature and moisture (rain and relative humidity) vary throughout the night; if calling were dependent on these factors (Bellis, 1957; Rome *et al*., 1992; Shoemaker *et al*., 1992; Bridges & Dorcas, 2000), we would also expect the calling pattern of frogs to vary (Caldwell, 1986). This might be true for *P. megacephalus*, *Microhyla* sp. and *Ra. psaltes*, as they called most intensely right after dark, and then tapered off throughout the night. Bridges & Dorcas (2000) suggest that phylogenetic relationships may explain nightly variation in calling patterns. In their study, both the hylids (*Acris* and *Hyla*) had a peak of calling between sunset and midnight. Their findings differ from what we observed for most of the species at our study site (e.g. *C. idiootocus*, *Rh. taipeianus*, *Ra. adenopleura*).

The majority of anurans at our study site had calling patterns that were similar across all four habitats; both *Ra. kuhlii* and *Ra. limnocharis* were unusual in exhibiting different patterns in different habitats. Schwartz & Wells (1984, 1985) reported that *Hyla microcephala* changed their calling in the presence of other species. Presumably, this allowed *H. microcephala* to increase their ability to communicate in an acoustically complex assemblage of frogs. In our study, *Ra. kuhlii* at the permanent pond called predominantly after midnight, probably in response to the presence of large numbers of *P. megacephalus* in the same pond. Different levels of calling intensity for *Ra. kuhlii* in the permanent marsh and ephemeral stream are probably related to different population sizes (Mohr & Dorcas, 1999). On the other hand, it is unclear why the calling pattern of *Ra. limnocharis* differed between the permanent and temporary ponds, when the species composition between these two habitats was rather similar.

We have demonstrated that the anuran species in Lien Hua Chih area of Taiwan exhibited seasonal variations in calling patterns that were closely related to reproductive activities. Nightly calling patterns also varied among species, although many species maintained relatively stable levels of calling intensity for many hours. Additional research on spatial and spectral components of acoustic assemblages in Lien Hua Chih is needed to shed light on how such a diverse assemblage of anurans is partitioning the acoustic resources in this subtropical forest.

Acknowledgements

This study was supported by National Science Council grants (NSC 91-2311-B-029-008 and NSC 93-2311-B-029-004) to Y.-C. Kam. We thank the staff of the Taiwan Forestry Research Institute at Lien Hue Chih field station for providing accommodation and permitting us to work at the station. We thank Liang Min-fang, Li Yun-chih, Wu Chi-tsung, Chen Hun-chuan, Lin Pei-yi, Huang Chia-Ru, Lin Kwan-yu, Chiu chia-te, Liu Chun-liang, Liau Wun-hau, Chung Min-fun, Lin Yi-tsian, Liao Chun-chin, Chung Cheng-shuo, Lin Shen-kuo, Chen-Su Huey and many others for their field and administrative assistance. We appreciate the comments and suggestions on an earlier draft of this manuscript by Kentwood Wells, Joan Fellers and Patrick Kleeman.

References

Aichinger, M. (1987). Annual activity patterns of anurans in a seasonal neotropical environment. *Oecologia* **71**, 583–592.

Bellis, E.D. (1957). The effects of temperature on salientian breeding calls. *Copeia* **1957**, 85–89.

Bevier, C.R. (1997). Breeding activity and chorus tenure of two neotropical hylid frogs. *Copeia* **1997**, 297–311.

Bridges, A.S. & Dorcas, M.E. (2000). Temporal variation in anuran calling behavior: implications for surveys and monitoring programs. *Copeia* **2000**, 587–592.

Caldwell, J.P. (1986). Selection of egg deposition sites: a seasonal shift in the southern leopard frogs, *Rana sphenocephala*. *Copeia* **1986**, 249–253.

Chen, T.C., Kam, Y.-C. & Lin, Y.S. (2001). Thermal physiology and reproductive phenology of *Buergeria japonica*

(Rhacophoridae) breeding in a stream and a geothermal hot spring in Taiwan. *Zool. Sci*. **18**, 591–596.

Chou, W.-H. & Lin, J.-Y. (1997). *Tadpoles of Taiwan*. Spec. Publ. No. **7***, Natl. Mus. Nat. Sci*. 98pp.

Corn, P.S., Muth, E. & Iko, W.M. (2000). A comparison in Colorado of three methods to monitor breeding amphibians. *Northwest. Nat*. **81**, 22–30.

Crump, M.L. (1974). Reproductive strategies in a tropical anuran community. *Misc. Pub.–Univ. Kansas, Mus. Nat. Hist*. **61**, 1–68.

Duellman, W.E. & Pyles, R.A. (1983). Acoustic resource partitioning in anuran communities. *Copeia* **1983**, 639–649.

Duellman, W.E. & Trueb, L. (1986). *Biology of amphibians*. New York: McGraw-Hill.

Fellers, G.M. (1979). Aggression, territoriality, and mating behaviour in North American treefrogs. *Anim. Behav*. **27**, 107–119.

Garcia-Rutledge, E.J. & Narins, P.M. (2001). Shared acoustic resources in an Old World frog community. *Herpetologica* **57**, 104–116.

Heyer, W.R., McDiarmid, R.W., Donnelly, M. & Hayek, L. (1994). *Measuring and monitoring biological diversity – standard methods for amphibians*. Washington, DC: Smithsonian Institution Press.

Howard, R.D. & Palmer, J.G. (1995). Female choice in *Bufo americanus*: effects of dominant frequency and call order. *Copeia* **1995**, 212–217.

Hsu, M.-Y., Kam, Y.-C. & Fellers, G.M. (2005). Effectiveness of amphibian monitoring techniques in a Taiwanese subtropical forest. *Herpetol. J*. **15**, 73–79.

Jorgensen, C.B., Shakuntala, K. & Vijayakumar, S. (1986). Body size, reproduction and growth in a tropical toad, *Bufo melanostictus*, with a comparison of ovarian cycles in tropical and temperate zone anurans. *Oikos* **46**, 379–389.

Kam, Y.-C. & Chen, T.C. (2000). Abundance and movement of a riparian frog (*Rana swinhoana*) in a subtropical forest of Guandau stream, Taiwan. *Zool. Stud*. **39**, 67–76.

Kam, Y.C., Chen, T.C., Yang, J.T., Yu, F.C. & Yu, K.M. (1998). Seasonal activity, reproduction, and diet of a riparian frog (*Rana swinhoana*) from a subtropical forest in Taiwan. *J. Herpetol*. **32**, 447–452.

Kam, Y.-C., Chuang, Z.-S. & Yen, C.-F. (1996). Reproduction, oviposition-site selection and larval oophagy of an arboreal nester, *Chirixalus eiffingeri* (Rhacophoridae), from Taiwan. *J. Herpetol*. **30**, 52–59.

Licht, L.E. (1969). Comparative breeding biology of the red-legged frog (*Rana aurora aurora*) and the western spotted frog (*Rana pretiosa pretiosa*) in southwestern British Columbia. *Can. J. Zool*. **47**, 505–509.

Lue, C.Y., Tu, M.C. & Shang, G. (1999). *A field guide to the amphibians and reptiles of Taiwan*. Taipei: Great Nature Magazine Publisher.

Menzies, J.I. (1963). The climate of Bo, Sierra Leone, and the breeding behavior of the toad, *Bufo regularis*. *J. W. Afr. Sci. Assoc*. **8**, 60–73.

Mohr, J.R. & Dorcas, M.E. (1999). A comparison of anuran calling patterns at two Carolina bays in South Carolina. *J. Elisha Mitchell Sci. Soc*. **115**, 63–70.

Parris, K.M., Norton, W.T. & Cunningham, B.R. (1999). A comparison of techniques for sampling amphibians in the forests of southeast Queensland, Australia. *Herpetologica* **55**, 271–283.

Pough, F.H., Magnusson, W.E., Ryan, M.J., Wells, K.D. & Taigen, T.L. (1992). Behavioral energetics. In *Environmental physiology of the amphibians*: 395–436. Feder, M.E. & Burggren, W.W. (Eds). Chicago, IL: The University of Chicago Press.

Pough, F.H., Taigen, T.L., Stewart, M.M. & Brussard, P.F. (1983). Behavioral modification of evaporative water loss by a Puerto Rican frog. *Ecology* **64**, 244–252.

Rome, L.C., Steven, E.D. & John-Alder, H.B. (1992). The influence of temperature and thermal acclimation on physiological function. In *Environmental physiology of the amphibians*: 183–205. Feder, M.E. & Burggren, W.W. (Eds). Chicago, IL: The University of Chicago Press.

Runkle, L.S., Wells, K.D., Robb, C. & Lance, S.L. (1994). Individual, nightly, and seasonal variation in calling behavior of the gray tree frog, *Hyla versicolor*: implications for energy expenditure. *Behav. Ecol*. **5**, 318–325.

SAS Institute Inc. (1996). *SAS/STAT user's guide*. Cary, NC: SAS Institution Inc.

Schwartz, J.J. & Wells, K.D. (1984). Interspecific acoustic interactions of the neotropical treefrog *Hyla ebraccata*. *Behav. Ecol. Sociobiol*. **14**, 211–224.

Schwartz, J.J. & Wells, K.D. (1985). Intra- and interspecific vocal behavior of the neotropical treefrog *Hyla microcephala*. *Copeia* **1985**, 27–38.

Shoemaker, V.H., Hillman, S.H., Hillyard, S.D., Jackson, D.C., McLanahan, L.L., Withers, P.C. & Wygoda, M.L. (1992). Exchange of water, ions, and respiratory gases in terrestrial amphibians. In *Environmental physiology of the amphibians*: 125–151. Feder, M.E. & Burggren, W.W. (Eds). Chicago, IL: The University of Chicago Press.

Sullivan, B.K., Ryan, M.J. & Verrell, P.A. (1993). Female choice and mating system structure. In *Amphibian biology*: 469–518. Heatwole, H. & Sullivan, B. (Eds). NSW, Australia: Surrey, Beatty and Sons.

Wells, K.D. (1977). The social behavior of anuran amphibians. *Anim. Behav*. **25**, 666–693.

Wiest, J.A. Jr. (1982). Anuran succession at temporary ponds in a post oak-savanna region of Texas. *US Fish Wildl. Res. Rep*. **13**, 39–47.

Zhao, E.-M. (1999). Distribution patterns of amphibians in temperate Eastern Asia. In *Patterns of distribution of amphibians*: 421–444. Duellman, W.E. (Ed.). Baltimore, MD: The Johns Hopkins University Press.

Zug, G.R. & Zug, P.B. (1979). The marine toad *Bufo marinus*: a natural history resume of native populations. *Smithsonian Contr. Zool*. **284**, 1–5.