Altitudinal Differences in Temporal Distribution, Spatial Preference and Timing of Breeding Climax of Frogs and Toads in the Central Taiwan

台灣中部蛙類與蟾蜍在時間分布、空間偏好與生殖高峰的海拔差異

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Abstract

This study compared temporal niche breadth, temporal niche overlap, spatial preference, and timing of breeding climax of frogs and toads in Wushikeng at 1,000m in elevation and in Chichi at 240m in the central Taiwan. The results showed that a species that had a wider temporal niche tended to have a wider niche overlap with other species. Also, the temporal niche breadths of the frogs and toads were significantly correlated with their temporal niche overlaps, while both niche breadths and overlaps were wider at the high elevation than at the low elevation. Most of the species expressed a spatial preference to either land or stream, but some showed no preference. An exception was *Rana latouchii*, which preferred land at the high elevation but stream at the low elevation. This was perhaps due to difference in water availability (precipitation) between the two elevations. The timing of breeding climax of most of the species at the high elevation was about two months later than that at the low elevation, except for *Buergeria robustus* the timing was the same at both elevations.

摘 要

本研究選擇台灣中部地區海拔1,000m之烏石坑與海拔240m之集集，比較兩地蛙類與蟾蜍的時間生態區位寬度、時間生態區位重疊度、空間偏好及生殖高峰期的海拔差異。結果顯示：一物種若有較寬之時間生態區位，該物種與其共棲物種間也將擁有較大的生態區位重疊度。此外，時

間生態區位寬度與時間生態區位重疊度呈現顯著性相關，且隨著烏石坑到集集海拔高度的降低，其寬度與重疊度亦下降。大部分物種在群聚中會表現出物種對空間偏好的特殊性，其選擇可以是陸域、溪流或沒有偏好。在此兩海拔物種空間偏好方面，唯一例外的是拉都希氏赤蛙，該蛙在烏石坑偏好出現在陸域，而在集集則偏好在溪流。其原因可能由於兩地海拔差異導致雨水的可利用性(降雨量)不同所致。在烏石坑大部分蛙類的生殖高峰比集集約晚2個月，只有褐樹蛙例外，該蛙在兩地擁有相同的生殖高峰。

Key words: amphibian, altitudinal differences, niche breadth, niche overlap, spatial preference

關鍵詞：兩棲類、海拔差異、生態區位寬度、生態區位重疊度、空間偏好

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Introduction

Animals tend to occupy wide ranges of temporal and spatial niches to maximize their resource utilization and to reduce interspecific competition. These niches differ among species, and are expressed by difference in their temporal appearance and/or spatial distribution (Begon *et al*. 1990). Frogs are poikilothermic animals and have physiological and behavioral adaptation to surrounding environments, causing the occurrence of altitudinal variation in temporal appearance, breeding period, and life history in many species (Pettus and Angleton 1967; Beattie 1985, 1987; Miaud *et al*. 1999; Lai *et al*. 2003). Also, the adult stage of frogs consists of the land phase for growth and the water phase for reproduction, coinciding with the seasonal changes in their surrounding environments. Different species of frogs usually choose different habitats for foraging, resting, and reproduction (Gao 1994; Chu 1996).

The purpose of this study was to determine interspecific and intraspecific differences in temporal and spatial niche utilization of frogs and toads, in terms of temporal niche breadth, temporal niche overlap, spatial preference, and the timing of breeding climax between two elevations: 1,000m in Wushikeng and 240m in Chichi in the central Taiwan.

Materials and Methods

Study stations

Two study stations representing two different elevations and temperature regimes were established: one in Wushikeng (24° 16' N, 120° 56' E) at an elevation of 1,000m and the other in Chichi (23° 51' N, 120° 44' E) at 240m (Fig. 1). The Wushikeng Station was located in the Central Mountain Range and covered with artificial coniferous and broad-leaf forests. The Chichi Station was located in the peripheral hills of the Central Mountain Range, and was an area

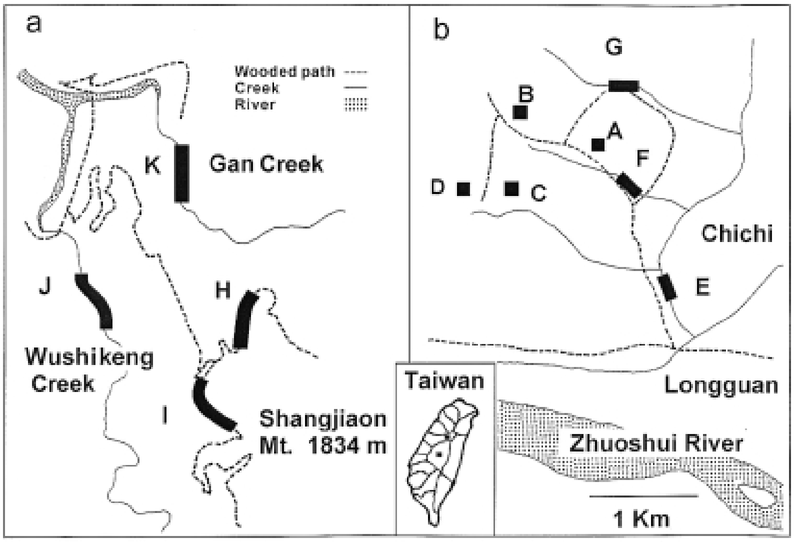

Fig. 1. The land sustations (A-D and H-I) and stream substations (E-G and J-K) at the Wushikeng Station (a) and the Chichi Station (b).

surrounded by working and abandoned orchards.

At each of the two stations, we designed land substation and stream substation for the study to represent, respectively, the habitat for land feeding phase and for stream breeding phase of frogs. The two substations at each station had the same size in the total area but differed in shape (design) due to different topography and stream conditions. At the Wushikeng Station, four 500m x 4m transects were established: two for each of the two substations (Fig. 1a). For the stream substation, one transect was along the bank of Wushikeng Creek and the other along Gan Creek. Both creeks had running water all the year round. Each of the two transects of the land substation was set in the mountain slopes of each of the creeks, where small, permanent and temporary pools were sparsely distributed. At the Chichi station, three transects, each 50m x 6m, were established along three small streams as the stream substation. These streams had flowing water in spring and summer, but was dry in fall and winter except after heavy rain. Four 15m x 15m plots encircling a small permanent pool were established as the land substation (Fig. 1b).

Survey method

Field surveys were conducted bimonthly from February 1997 to December 1998 at the Wushikeng Station, and from February 2000 to December 2001 at the Chichi Station. For each survey the visual encounter method (Heyer *et al*. 1994) was used to record the species and the number of adult frogs observed. Breeding behavior, including mating and spawning, was noted to determine the breeding period. The month with the highest numbers of mating individuals observed in the breeding period for a species was treated as the breeding climax for that particular species. The surveys were conducted one hour after sunset to reduce the influence of illumination.

Data analyses

Numbers of adult frogs of each species counted at each substation in the same month were summed up for two successive years as the relative abundance of the species for that month at that particular substation. The seasonal pattern in abundance was compared among species. In this study we regarded abundance of each species of frogs in different investigated months as its temporal niches, and abundance in difference between land and stream habitats as its spatial niches.

The temporal niche breadth that expresses the scope of utilizing a temporal resource by a species was measured by the following formula (Levins 1968):

$$B_i = 1/\sum_{j=1}^{n} P_{ij}^2 \text{.......................................} (1)$$

where B_i is niche breadth of species i; P_{ij} is the proportion of species i found in month j (j = 1 to 6, representing February to December) of the survey period.

The temporal niche overlap that expresses a degree of overlap in a temporal resource between two species was measured by the following formula (Pianka 1973):

$$\alpha_{yx} = (\sum_{j=1}^{n} P_{xj} * P_{yj}) / \sqrt{\sum_{j=1}^{n} P_{xj}^2 * \sum_{j=1}^{n} P_{yj}^2} \text{...........} (2)$$

where α_{yx} is niche overlap between species x and species y; $P_{xj(\text{or } yj)}$ is proportion of x (or y) species found in month j in the survey period. The α_{yx}-value is a symmetric measure of overlapping, so that an overlap of species x to species y is identical to the overlap of species y to species x. It ranges from 0 (no overlap: no temporal niche shared in common by species x and species y) to 1 (100% overlap: the same temporal niche share by species x and species y).

The proportion of total individuals of each species was compared between the land and stream substations by the *Chi-square* test to determine the homogeneity of individual distributions within and between the two substations. The spatial preference of each species was then defined as the species with terrestrial, aquatic or no preference.

Meteorological data

The mean monthly air temperatures from February 1997 to December 1998 and February 2000 to December 2001 were obtained from the Wushikeng meteorological station for the Wushikeng Station and from the Endemic Species Research Institute in Chichi for the Chichi Station. The annual average temperature at Wushikeng was 18.5℃ (range from 12.5℃ to 23.2℃), that was 4.4℃ lower than 22.9℃ (range from 17.0℃ to 27.8℃) at Chichi (Fig. 2).

Results

Temporal niche breadth

At the Wushikeng Station 11 species were found, and 6 species had sufficient data for calculating B_i-values, whereas at the Chichi Station 16 species were found, and 12 species were calculated for the B_i-values (Table 1). The species diversity and abundance were higher at the Chichi Station than those at the Wushikeng Station.

At Wushikeng, *Bufo bankorensis* had the widest temporal niche breadth with the B_i-value of 5.53, whereas *Rana sauteri* had the narrowest value of 2.14. At Chichi the widest B_i-value was

Table 1. Temporal niche breadths (B_i-values) calculated for each species of frogs and toads based on the number of individuals counted at the Wushikeng Station, 1997-1998 and at the Chichi Station, 2000-2001 (total numbers of individuals observed in parentheses)

Species	Wushikeng	Chichi
Bufo bankorensis	5.53 (488)	1.55 (52)
Rhacophorus moltrechti	4.53 (76)	3.32 (146)
Buergeria robustus	3.44 (109)	3.50 (81)
Rana sauteri	2.14 (67)	1.50 (298)
Rana latouchii	4.70 (135)	3.56 (595)
Rana swinhoana	4.27 (150)	
Polypedates megacephalus	* (5)	3.25 (143)
Chirixalus eiffingeri	* (6)	3.76 (67)
Buergeria japonicus	* (3)	* (6)
Rana kuhlii	* (2)	* (2)
Chirixalus idiootocus	* (5)	
Bufo melanosticus		5.10 (53)
Rana limnocharis		3.55 (23)
Rana guentheri		3.90 (38)
Microhyla ornata		2.74 (35)
Microhyla heymonsi		2.31 (19)
Rana rugulosa		* (1)
Micryletta steinegeri		* (1)

* Numbers too small to calculate B_i-values.

for *Bufo melanosticus* at 5.10 and the narrowest value was for *R. sauteri* at 1.50 (Table 1). Five species whose B_i-values were measured were found at both Wushikeng and Chichi stations. Four of them had wider values at Wushikeng than those at Chichi. They were *B. bankorensis*, *R. sauteri*, *Rana latouchii*, and *Rana swinhoana*, whereas *Buergeria robustus* had fairly similar values between the two stations.

Temporal niche overlap

The niche overlaps expressed by α_{yx}-values were compared among the six species, of which B_i-values were calculated for the Wushikeng Station. The α_{yx}-value was highest (0.98) between *Rhacophorus moltrechti* and *R. latouchii*, and lowest (0.15) between *Rh. moltrechti* and *R. sauteri* at Wushikeng (Table 2). The average α_{yx}-values (Table 2) and the B_i-values at Wushikeng (Table 1) were significantly correlated (r-value =0.93, df=5, p<0.01).

A similar relationship in niche overlap was also found at Chichi (Table 3). Among 12 species with B_i-values (Table 1), the α_{yx}-value

Table 2. Niche overlaps (α_{yx}-values) among different species of adult frogs and toads at the Wushikeng Station

Species	1	2	3	4	5	6	Average
1 *Bufo bankorensis*	-	0.79	0.56	0.71	0.81	0.72	0.72
2 *Rhacophorus moltrechti*		-	0.77	0.15	0.98	0.77	0.69
3 *Buergeria robustus*			-	0.16	0.78	0.77	0.61
4 *Rana sauteri*				-	0.20	0.35	0.31
5 *Rana latouchii*					-	0.71	0.70
6 *Rana swinhoana*						-	0.66

was highest (1.00) between *Polypedates megacephalus* and *B. robustus*, and lowest (0.04) between *R. sauteri* and *Microhyla heymonsi* (or *Microhyla ornata*). Like the case at Wushikeng, the average α_{yx}-values (Table 3) were also significantly correlated with the B_i-values at Chichi (Table 1) (r-value =0.73, df=11, p<0.01).

Spatial preference

At the Wushikeng Station, the number of individuals observed at the stream substation was significantly higher than at the land substation for *B. bankorensis*, *B. robustus, R. sauteri and R. swinhoana*, suggesting that these four species preferred the stream habitat to the land habitat (Table 4). In contrast, *Rh. moltrechti* and *R. latouchii* prefered land to stream. At the Chichi Station *Rh. moltrechti, P. megacephalus, M. ornata and M. heymonsi* preferred land to stream, whereas *B. bankorensis, B. robustus, R. sauteri* and *R. latouchii* preferred stream to land. *Chirxalus eiffingeri, B. melanosticus, Rana limnocharis* and *Rana guentheri* showed no special preference to either land or stream (Table 4).

Breeding climax

The months of breeding climax of five species of frogs and toads observed at both two stations are shown in Table 5. The peak breeding seasons of *B. bankorensis, Rh. moltrechti, R. sauteri* and *R. latouchii* at Wushikeng were two months later than those at Chichi. An exception was that *B. robustus* had the same breeding climax season at both stations.

Discussion

Temporal niche breadth

Levins (1968) proposes that niche breadth be estimated by measuring the uniformity of distribution of individuals among the resource states. Niche breadth scores can be used to designate species as a generalist with a wide tolerance to environments or a specialist with a narrow tolerance to the environment (Dash and Mahanta 1993).

In this study *B. bankorensis* had the widest temporal niche breadth at the Wushikeng Station but not at the Chichi Station (Table 1). This species is widely distributed in the Central Mountain Range and is observed at elevations

Table 3. Niche overlaps (α_{yx} -values) among different species of adult frogs and toads at the Chichi Station

Species	1	2	3	4	5	6	7	8	9	10	11	12	Average
1 Bufo bankorensis	-	0.81	0.16	0.29	0.82	0.14	0.16	0.33	0.11	0.19	0.12	0.05	0.29
2 Rhacophorus moltrechti		-	0.25	0.35	0.93	0.24	0.22	0.47	0.28	0.27	0.22	0.13	0.38
3 Buergeria robustus			-	0.10	0.36	1.00	0.98	0.89	0.91	0.91	0.91	0.89	0.67
4 Rana sauteri				-	0.62	0.06	0.10	0.18	0.20	0.13	0.04	0.04	0.19
5 Rnan latouchii					-	0.33	0.32	0.53	0.41	0.35	0.30	0.25	0.47
6 Polypedates megacephalus						-	0.99	0.91	0.90	0.94	0.93	0.88	0.67
7 Chirixalus eiffingeri							-	0.93	0.90	0.97	0.95	0.90	0.67
8 Bufo melanosticus								-	0.92	0.96	0.96	0.88	0.72
9 Rnan limnocharis									-	0.87	0.95	0.97	0.68
10 Rana guentheri										-	0.95	0.86	0.67
11 Microhyla ornata											-	0.97	0.66
12 Microhyla heymonsi												-	0.62

Table 4. Spatial preference to land or stream for adults of the frogs and toads at the Wushikeng and Chichi stations (data, numbers of individuals observed)

Species	Wushikeng		Chichi	
	Land	Stream	Land	Stream
Bufo bankorensis *	156	332	1	51
Rhacophorus moltrechti *	67	9	140	6
Buergeria robustus *	1	108	0	81
Rana sauteri *	2	65	2	296
Rana latouchii *	110	25	172	423
Rana swinhoana *	32	118		
Polypedates megacephalus *			141	2
Chirixalus eiffingeri			24	43
Bufo melanosticus			27	26
Rana limnocharis			12	11
Rana guentheri			16	22
Microhyla ornata *			32	2
Microhyla heymonsi *			18	0

* Significant at 0.1% level (χ^2-test, p<0.001).

Table 5. The month of breeding climax of five species of frogs and toads commonly observed at the Wushikeng and Chichi stations

Species	Wushikeng	Chichi
Bufo bankorensis	February	December
Rhacophorus moltrechti	February	December
Buergeria robustus	August	August
Rana sauteri	December	October
Rana latouchii	February	December

above 500m in Taiwan. It was found at the Wushikeng Station all the year round, but was mainly observed in the cold months of the year at the Chichi Station. Its abundance was highest in December, constituting 82% of the total number of individuals observed in a year. At the Chichi Station, the climate may be too hot for its breeding activity except in winter. This species may migrate from high elevation to low elevation with the dropping of temperature in winter (Huang 1991).

Based on lengths of breeding durations, Wittenberger (1981) divides animals into two breeding types: explosive breeding and prolonged breeding. *B. bankorensis* at the Chichi Station (low elevation) could be categorized as a specialist with explosive breeding, whereas at the Wushikeng Station (high elevation) it was a generalist with prolonged breeding. In contrast to *B. bankorensis*, *R. sauteri* had the narrowest temporal niche breadth among the frogs at both stations (Table 1). It is an explosive breeder, and is known to have a short breeding period (Kuramoto *et al*. 1984; Lai *et al*. 2003). In the mountain region of Taiwan, *R. sauteri* may be divided into three populations according to their breeding seasons (Lai *et al*. 2003). The population at elevations of 240m to 1,000m found in this study belongs to the fall breeding population.

In this study the B_i-values of the species at the Wushikeng Station were generally higher than those of the same species at the Chichi Station (Table 1), suggesting that the temporal niche breadth of a species increased with the elevation up to 1,000m. There were 12 species at Chichi, but only 6 species at Wushikeng, suggesting that the species diversity of frogs decreased with the increase in elevation. Higher species diversity in the frog community at the Chichi Station, as compared to that of the Wushikeng Station, might be also a factor that reduced the niche breadth of the species (Table 1), but at the same time, increased niche overlap among species (Tables 2 and 3).

Amphibians show physiological and behavioral responses to fluctuations in surrounding environments, such as temperature (Brattstrom 1979; Hutchison and Dupre 1992), light illumination (Church 1961), and water availability (Dole and Durant 1974; Harris 1975; Pough *et al*. 1983; Cree 1989). Among these environmental factors, temperature has been considered to be the most important modulator for the amount of time available for activity of frogs (Tracy and Christian 1986). The monthly mean temperatures at Wushikeng were significantly lower than that at Chichi, but the monthly mean temperature curves at the two stations were similar (Fig. 2). The lower temperature at Wushikeng comparing to that at Chichi might be an important factor causing the lower species diversity, the wider temporal niche breadths (B_i) (Table 1), and wider temporal niche overlaps (α_{yx}) for the species (Tables 2 and 3). The only exception was *B. robustus* that had similar B_i-value between Wushikeng and Chichi station. Chu (1996) suggests that in the northern Taiwan, *B. robustus* has the same active season in spring and summer at elevations of 350m and 700m, similar to the case found for the species at elevations of 240m and 1,000m in this study.

Temporal niche overlap

Niche overlap value has been found to be a function of the relative abundance of frogs in the same niche dimension (Dash and Mahanta 1993). The lowest value of temporal niche overlap was found between *Rh. moltrechti* and *R. sauteri* at the Wushikeng station and between *R. sauteri* and *M. heymonsi* (or *M. ornata*) at the Chichi Station (Tables 2 and 3). The lowest value at each station suggested that the temporal niches might be an ecological character useful in niche differentiation between the two species. On the other hand, the highest value of temporal

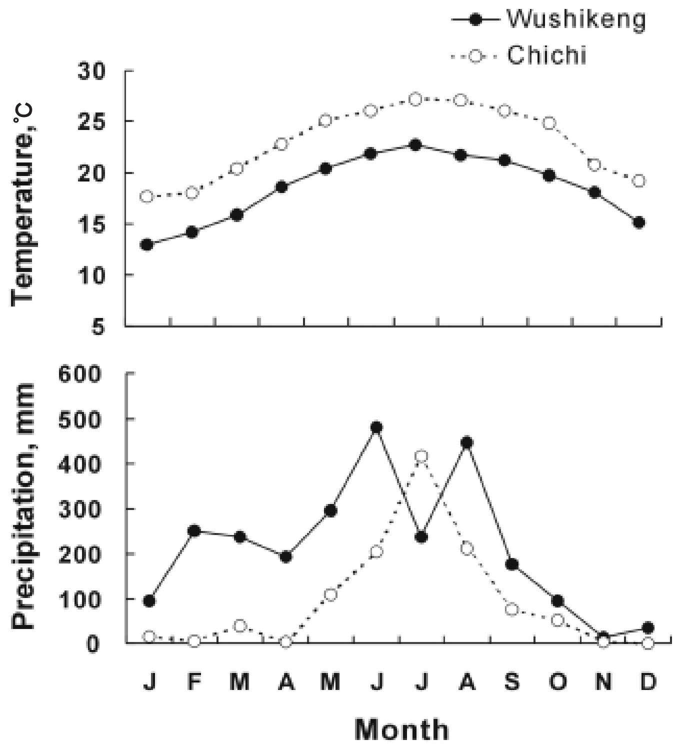

Fig. 2. Monthly average temperature and precipitation at the Wushikeng Station (1997-1998) and at the Chichi Station (2000 -2001).

niche overlaps was observed between *Rh. moltrechti* and *R. latouchii* at Wushikeng, and between *P. megacephalus* and *B. robustus* at Chichi (Tables 2 and 3). The highest value might suggest the presence of different niche dimension to reduce their competition in the frog community at each of the two stations. At Wushikeng *R. latouchii* was usually found to associate with the bottom substrates of still water bodies, whereas *Rh. moltrechti* was predominantly associated with aquatic vegetation. At Chichi *P. megacephalus* preferred land habitat, but *B. robustus* to the stream habitat (Table 4).

In this study *B. bankorensis* and *B. melanostictus* were found to have the widest temporal niche breadths (Table 1) with the highest values of average temporal niche overlaps (Tables 2 and 3) at Wushikeng and Chichi, respectively. The two species have wide ranges of tolerance to environmental gradients, so that they are easy to overlap with other species (Dash and Mahanta 1993).

Spatial preference

Based on the difference in abundance of adults at the land and stream substations (Table 4), *Rh. moltrechti, P. megacephalus, M. ornata* and *M. heymonsi* were considered as the frogs that preferred terrestrial habitats, whereas *B. bankorensis, B. robustus, R. sauteri,* and *R. swinhoana* preferred aquatic habitats. *C. eiffingeri, B. melanosticus, R. limnocharis* and *R. guentheri* did not show preference to either land or stream. Only *R. latouchii* that had different habitat preference between the two stations: stream preference at the Chichi Station and terrestrial preference at the Wushikeng Station. It seems that *R. latouchii* possess a strong flexibility in adaptation to the different habitats. We suspected that the difference in precipitation at different elevations affected water availability, and *R. latouchii* responded to the difference by changing its spatial preference. At the Wushikeng Station where precipitation was high and stream flow was faster all the year round, the frog tended to live in the land with still water bodies (Fig. 2). On the other hand, at the Chichi Station, where precipitation was low and the streams often dried up in fall or winter, the frog was only found in the streams with slow flowing water.

Breeding season

Beattie (1985) recorded the first spawning dates of *Rana temporaria* in a series of ponds over four years, and found that the initiating spawning of this species was delayed by six days for every 100m increase in altitude. Apparently, the timing of breeding is probably controlled not only by circannual endogenous rhythm but also by elevation. In this study, the elevation difference between the two stations was 850m. According to Beattie (1985), the frogs at the Wushikeng might delay their first spawning for 52 days. Although we did not record the time of first spawning, this phenomenon might indicate the lateness of breeding climax by two months at Wushikeng as compared to that at Chichi (Table 5).

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