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Nest Choice and Breeding Phenology of an Arboreal-Breeding Frog, *Kurixalus eiffingeri* (Rhacophoridae), in a Bamboo Forest

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Yi-Shian Lin and Yeong-Choy Kam (2008) Nest choice and breeding phenology of an arboreal-breeding frog, *Kurixalus eiffingeri* (Rhacophoridae), in a bamboo forest. *Zoological Studies* **47**(2): 129-137. Nest choice and reproductive phenology of *Kurixalus eiffingeri* (formerly known as *Chirixalus eiffingeri*) were studied in a bamboo tree habitat in the Chitou area, central Taiwan from Feb. 2004 to Mar. 2005. We visited the study site weekly where we searched for newly laid egg clutches in stumps during the daytime and recorded the oviposition site characteristics. We also counted the number of stumps with standing water and measured the water depth in every stump. At night, we searched for frogs on the forest floor and every stump. Results showed that changes in the water level of the bamboo cups were closely associated with rainfall patterns, and a step-wise regression revealed that the number of stumps containing water and the water level of those stumps were the most important factors influencing the breeding activity of *K. eiffingeri*. Stumps differed in height, diameter, cup depth, and water depth. In addition, the water level of every stump fluctuated over time, and the pattern and amount of water level fluctuation varied among stumps. Results showed that *K. eiffingeri* is selective about oviposition sites, which is probably related to the water resource in the bamboo cups that varies greatly among stumps and is the most critical resource for the survival of embryos and tadpoles. However, stumps that were used 1, 2, 3, or 4 times did not significantly differ in characteristics of stumps, suggesting that other factors may be important in determining the reuse of stumps. http://zoolstud.sinica.edu.tw/Journals/47.2/129.pdf

Key words: Anura, *Chirixalus eiffingeri*, Container habitats, Nest choice, Phytotelmata.

Arboreal water pools (i.e., phytotelmata), which can be found in tree holes and cavities, bamboo stumps, bromeliad leaf axils, nut capsules, and other sites, are unique and isolated microhabitats that are more common than originally thought (Laessle 1961, Wassersug et al. 1981, Lannoo et al. 1987, Caldwell 1993, Kam et al. 1996, Lehtinen et al. 2004). Although these habitats contain small volumes of water, they serve as important water resources for a wide array of animals which forage, find refuge, disperse, and breed in them. Arboreal pools receive only rain water, thus the timing and patterns of rainfall play key roles in shaping the biological activity of animals in these microhabitats (Kitching 2000). Any delay or advance in the rainy season could potentially influence the population dynamics and even the community structure and functions of plants and animals that rely on these water resources. It is generally agreed that rainfall is intimately linked to the hydrological conditions of arboreal pools; however, the dynamic relationship between these 2 variables has seldom been examined (Kingsolver 1979, Kitching 2000).

In the cloud-forest zone of central Taiwan, local farmers grow bamboo, *Phyllostachys edulis* and *Sinocalamus latiflorus*, for many commercial purposes. The bamboo trees are periodically cut and the stumps remain for several years before disintegrating. After they are cut, the hollow bamboo stumps receive rain water and form discrete, arboreal pools that are scattered on the floor of the bamboo forest. *Kurixalus eiffingeri* (formerly known as *Chirixalus eiffingeri*) (Frost

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et al. 2006), a rhacophorid, uses these bamboo stumps as breeding sites, and it lays its eggs on the inner walls of bamboo stumps above the water line. In this study, we assessed the dynamic relationships of rainfall, hydrological conditions of the bamboo stumps, and stump characteristics with the breeding phenology of and nest choice by *K. eiffingeri*. We hypothesized that the water resources in these arboreal pools are important to *K. eiffingeri*. Based on this hypothesis and the distinct dry and wet seasons at our study site, we predicted that the frog’s activities and breeding phenology would be closely related to rainfall patterns. In addition, we also predicted that the amount of water received and water fluctuations would vary among stumps, and these differences would affect nest choice by *K. eiffingeri*.

MATERIALS AND METHODS

Study site

All experiments were conducted in a bamboo forest at the Experimental Forest of National Taiwan University, Chitou (elevation 1016 m, approximately 23°39'20"N, 120°48'10"E), Nantou County, central Taiwan. Chitou receives approximately 3 m of rainfall annually. The rainfall pattern in the study area is characterized by a wet (Mar.-Sept.) and dry (Oct.-Feb.) season. Heavy rains in the spring are associated with the “plum rains” and in summer with typhoons and afternoon thunderstorms. The mean annual air temperature is about 17°C (Fig. 1).

Study animals

The rhacophorid tree frog, *K. eiffingeri*, is a small frog with a snout-vent length of 30-40 mm. It is endemic to Taiwan and 2 nearby, small islands, Iriomote and Ishigaki of Japan (Kuramoto 1973). During the breeding season (Feb.-Aug.), male *K. eiffingeri* frogs call from bamboo stumps. Fertilized eggs are deposited above the waterline on the inner walls of tree holes or bamboo stumps (Kuramoto 1973, Kam et al. 1998a). Upon hatching, tadpoles drop into the pool of water where they grow and develop until metamorphosis. Male frogs exhibit paternal care during the embryonic stages (ca. 10-14 d), and they leave the stumps after the embryos have hatched. Tadpoles are obligatorily oophagous and are fed by females that lay unfertilized, trophic eggs directly into the water, in the absence of male frogs (Ueda 1986). The pools of water in the bamboo stumps also contain microorganisms (euglenoids, diatoms, paramecia, *Chlorella*, and rotifers) and the larvae of invertebrates (order Diptera: Culicidae, Chironomidae, and Tipulidae). These organisms in the pools do not appear to be directly associated with the tadpoles, as they are neither food for nor predators of the tadpoles, and they do not compete with tadpoles for the trophic eggs (Ueda 1986, Kam et al. 1996).

Experimental protocol

We selected a 20 x 40 m bamboo tree habitat as our study site and marked every bamboo stump before the breeding season. Three sides of the plot were surrounded by broadleaf forests, and the remaining side was separated from other bamboo forests by a 6 m unpaved road. Bamboo formed a fairly dense canopy, and herbs and a few shrubs were found at ground level. Bamboo trees grew to an average of 12 m or higher.

We visited the bamboo forest once a week. We conducted a direct sampling of the study plot during the nighttime (19:00-23:00) when we gently scratched the forest floor with a stick and also visually checked every stump for frogs. We toe-clipped and recorded the age (adult or juvenile), sex, and snout-vent length (SVL) of every captured individual. SVL was measured to the nearest 0.01 mm using digital calipers. Frogs showed sexual dimorphism in body size; the SVL of female frogs caught in the bamboo forest was seldom < 32 mm

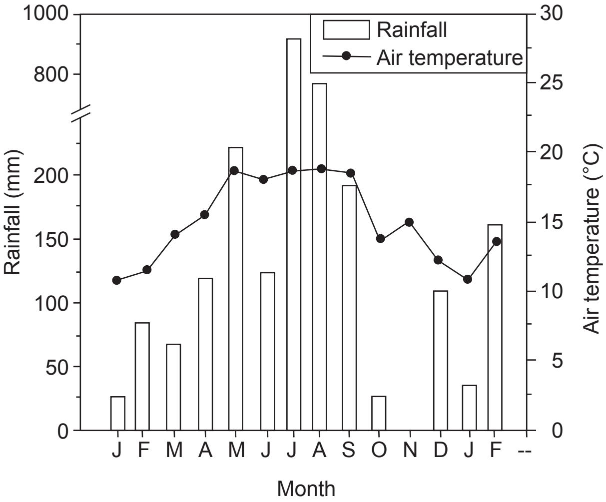

Fig. 1. Monthly mean air temperature and precipitation at Chitou, Taiwan from Jan. 2004 to Feb. 2005.

(37.98 ± 3.83 mm for females and 32.83 ± 2.85 mm for males) (Chen et al. 2007). Adult male frogs were identified by the presence of vocal sacs and/or nuptial pads. Frogs with an SVL exceeding 32 mm and lacking a vocal sac were classified as adult females, whereas frogs with an SVL of < 32 mm and lacking a vocal sac were classified as subadults or juveniles (Chen et al. 2007).

During the daytime, we searched for newly laid egg clutches. Because the developmental time for eggs to hatch is about 9-14 d, we were confident that weekly visits allowed us to locate virtually every newly deposited egg clutch. We recorded the oviposition site characteristics including (1) bamboo stump height (measured from the base of the stump to the cup opening), (2) inner diameter of the cup, (3) cup depth, and (4) water depth. Each week, we counted the number of stumps with standing water in the plot and measured the water depth of every stump. The water level of each stump fluctuated throughout the study period; thus, at the end of study, we averaged the water depth of each stump. In addition, we identified the maximum and minimum water depths of each stump. Using these values, we averaged the mean, maximum, and minimum water depth of all stumps in the study plot. For stumps that were never used by

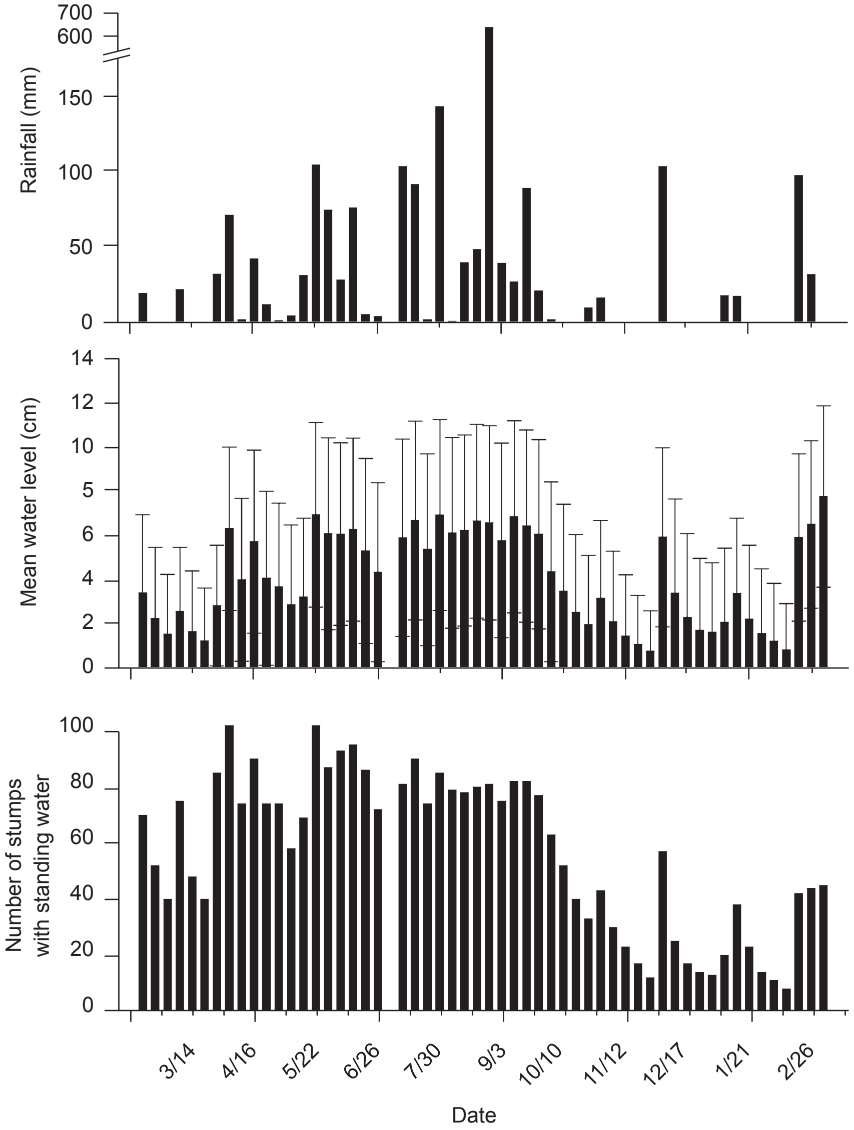

Fig. 2. Weekly rainfall, mean water depth (± SD), and number of stumps with standing water from Feb. 2004 to Mar. 2005. Mean water depth was calculated based on measurements of all stumps on each sampling day. The absence of data on July 3 was due to inaccessibility of the study site caused by rockslides.

frogs, we measured the bamboo trunk height, inner diameter of the cup, and cup depth at the end of the breeding season.

Statistical analyses

We performed statistical analyses using SAS (SAS Institute 1996). We used the Spearman correlation coefficient to assess correlations of the number of frogs with the number of stumps with standing water, mean water depth, air temperature, and rainfall. We further used a stepwise regression to determine the relative importance of each variable (number of stumps with standing water, mean water depth, air temperature, and rainfall) in predicting the number of frogs. We also used a stepwise regression to determine the relationships between water fluctuations in the stumps and other variables (stump height, stump diameter, and cup depth). We used a multivariate test, Hotelling's T^2 test, to assess if any evidence of a statistical difference existed between used and unused stumps when all 5 variables were considered together. Oviposition site variables were further analyzed using analysis of variance (ANOVA), and the significance level was adjusted using the sequential Bonferroni method (Rice 1989). Variables were either log-transformed (cup depth and water depth) or square-root-transformed (maximum and minimum water depths) to meet the parametric assumption of normality. A *p* value of 0.05 was considered statistically significant.

RESULTS

Changes in the water levels of bamboo cups followed rainfall patterns in that a heavy rain immediately increased water levels in the bamboo cups (Fig. 2). During the dry season, the water level in the bamboo cups rapidly dropped, probably due to evaporation. The mean water depth and the number of bamboo cups with standing water were significantly correlated with rainfall (r_s = 0.82, $p < 0.0001$, n = 54; and r_s = 0.76, $p < 0.0001$, n = 54, respectively; Fig. 2).

We observed 373 frogs (89 males and 38 females) in total; many individuals were repeatedly captured during the 13 mo study period. The majority of frogs were observed between Mar. and Aug., and frog activity was significantly correlated with the number of egg clutches found (r_s = 0.71, $p < 0.0001$, n = 55, Fig. 3). The number of frogs counted each week was significantly correlated with the number of stumps with standing water (r_s = 0.66, $p < 0.0001$, n = 55), mean water depth (r_s = 0.42, p = 0.0015, n = 55), air temperature (r_s = 0.36, p = 0.063, n = 54), and rainfall (r_s = 0.42,

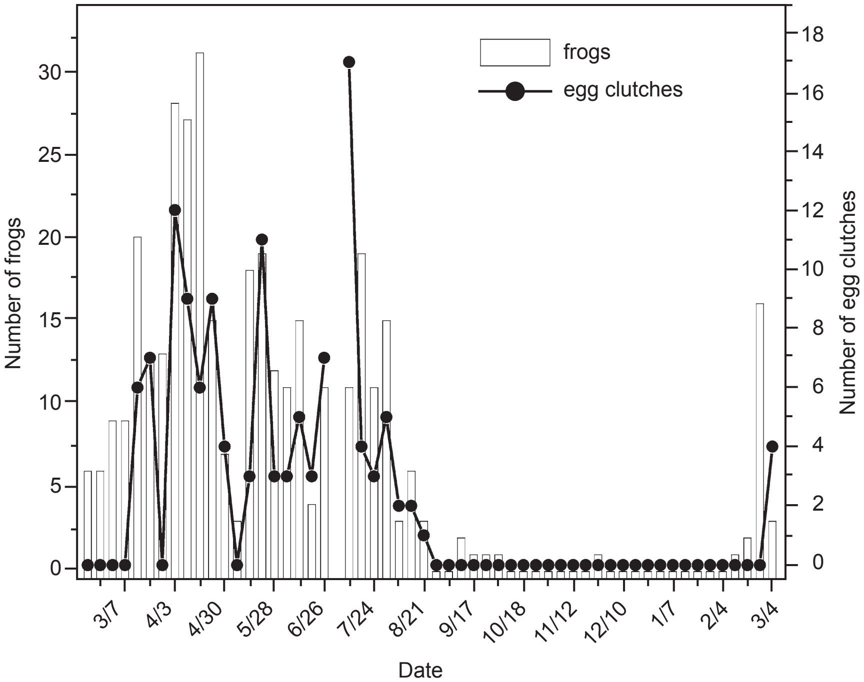

Fig. 3. Numbers of frogs and egg clutches found weekly from Feb. 2004 to Mar. 2005.

$n = 54$, $p = 0.0012$). However, a forward stepwise regression analysis showed that the number of frogs was significantly correlated with the number of stumps with standing water (partial $r^2 = 0.34$, $p < 0.0001$) and mean water depth (partial $r^2 = 0.06$, $p = 0.0329$).

Stumps significantly differed in height (mean 36.6 ± 14.5 cm, $n = 107$, coefficient of variation (CV) = 39.6%, Shapiro-Wilk test, $W = 0.965$, $p = 0.0093$), diameter (6.99 ± 1.31 cm, $n = 107$, CV = 18.7%, $W = 0.972$, $p = 0.03$), and cup depth (10.84 ± 5.91, $n = 107$, CV = 54.5%, $W = 0.972$, $p < 0.0001$) and were not normally distributed. Cup depth varied among stumps, with more stumps having shallow cups (i.e., < 20 cm in depth), and only 10% of cups deeper than 20 cm.

The water level of every stump fluctuated over time, and the pattern and amount of water level fluctuations varied among stumps, as illustrated in figure 4. For example, the patterns of water level fluctuations in stumps 5 and 232 were similar during the wet season but differed in the dry season. Another example is that the water level of stump 217 steadily decreased from Apr. to the end of the wet season (i.e., Sept.), whereas that of stump 5 steadily increased during the same period of time (Fig. 4). To further understand the mechanisms underlying water level fluctuations of stumps, we calculated the CV of water level fluctuations of each stump for the study period (Fig. 5). For the majority of stumps, the CV of water

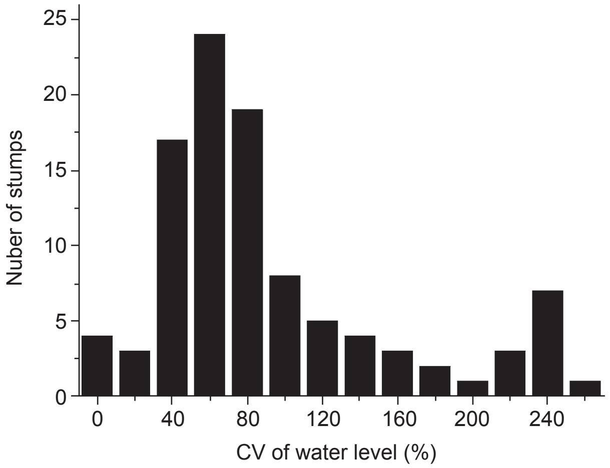

Fig. 5. Frequency distribution of the coefficient of variation (CV) of water levels in all stumps. We measured the water depth of each bamboo cup weekly from Feb. 2004 to Feb. 2005 and calculated its CV at the end of the study period.

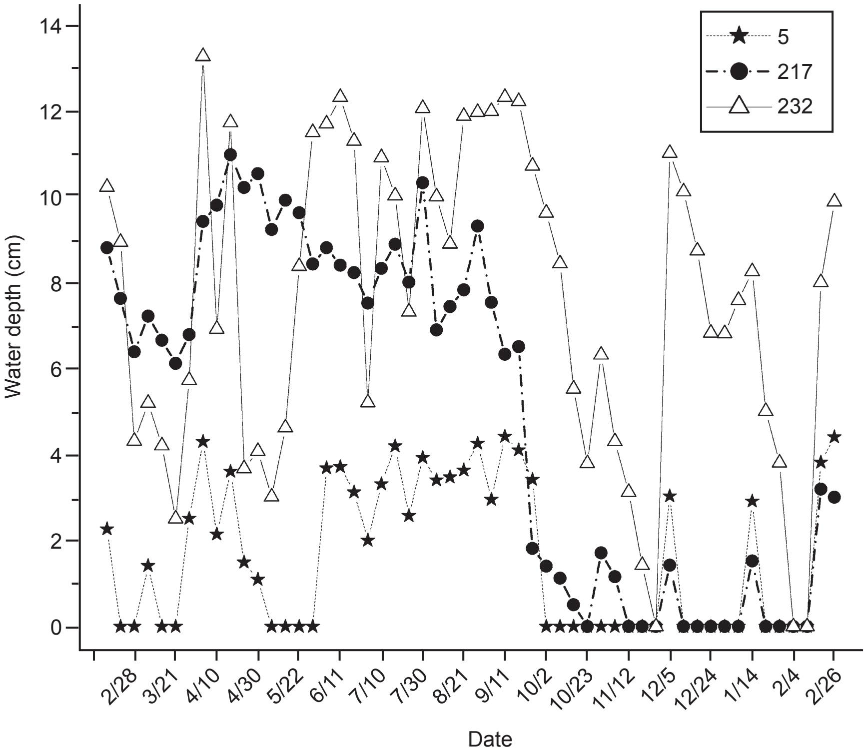

Fig. 4. Fluctuations in water levels of 3 stumps (nos. 5, 217, and 232) from Feb. 2004 to Feb. 2005.

fluctuations was between 40% and 80%. The CV of water fluctuations of stumps was significantly correlated with stump height ($r_s = -0.32$, $p < 0.001$, $n = 101$) and cup depth ($r_s = -0.37$, $p = 0.0001$, $n = 101$) but not with stump diameter ($r_s = -0.04$, $p = 0.640$, $n = 101$). A forward stepwise regression analysis also showed that the CV of water fluctuations of stumps was significantly correlated with stump height (partial $r^2 = 0.14$; $p = 0.0002$) and cup depth (partial $r^2 = 0.04$; $p = 0.0317$).

Frogs used 58.5% of available stumps (62/106 stumps) as oviposition sites. A multivariate comparison between used and unused stumps statistically differed (Hotelling-Lawley Trace, $F_{5,95} = 15.76$, $p < 0.0001$). Results of the univariate comparisons showed that the stump height, cup depth, maximum water depth, minimum water depth, and mean water depth of used stumps significantly differed from those of unused stumps (Table 1).

Among the stumps that were used, not all of them were used equally, as shown by the fact that 43%, 28%, 16%, and 11% of stumps were used 1, 2, 3, and 4 times, respectively. No measurements of stump characteristics statistically differed among groups (Table 2).

DISCUSSION

The reproductive activity of anurans is generally governed by environmental moisture and temperature (Duellman and Trueb 1986). In temperate areas, temperature and moisture are considered to be the major environmental variables that determine reproduction, whereas in tropical areas, many anurans are opportunistic and breed whenever sufficient water is available (Crump 1974, Duellman and Trueb 1986). In subtropical Taiwan, many amphibians are thought to have dispersed from tropical and temperate regions of mainland Asia to the island via land bridges during periods of lower sea levels in the Pleistocene (Zhao 1999). The assemblage of species that became established on Taiwan is unique in that there are spring-summer, fall-winter, and year-round breeders, because reproductive activities of some species are sensitive to temperature, whereas other species are sensitive to moisture or water availability (Hsu et al. 2006). *Kurixalus eiffingeri* in Chitou breeds in winter (Feb.), suggesting that temperature is not a limiting factor for breeding (Kam et al. 1996). In this study, a step-wise regression revealed that the number of stumps

Table 1. Comparison of site characteristics between used and unused bamboo stumps by *Kurixalus eiffingeri*. An asterisk with a *p* value indicates a statistical difference using the Bonferronic sequential method

Variable	Used stumps ($n = 57$)	Unused stumps ($n = 44$)	F	p
Stump height (cm)	40.2 ± 15.1	30.9 ± 12.3	11.11	0.0012*
Cup diameter (cm)	7.1 ± 1.0	6.9 ± 1.3	1.36	0.2467
Cup depth (cm)	12.5 ± 5.6	8.2 ± 5.0	23.76	< 0.0001*
Maximum water depth (cm)	9.8 ± 3.5	5.5 ± 3.1	48.74	< 0.0001*
Minimum water depth (cm)	1.43 ± 2.58	0.24 ± 1.05	12.34	0.0007*
Water depth (cm)	6.17 ± 3.09	2.18 ± 2.17	77.48	< 0.0001*

Table 2. Comparison of site characteristics between stumps that were used 1, 2, 3, and 4 times by *Kurixalus eiffingeri*. *F* and *p* represent *F* values and significant probabilities, respectively

Variable	Once ($n = 25$)	Twice ($n = 16$)	Three times ($n = 9$)	Four times ($n = 6$)	F	p
Stump height (cm)	41.1 ± 19.2	37.3 ± 11.5	42.0 ± 11.5	42.1 ± 9.4	0.30	0.822
Cup diameter (cm)	7.1 ± 1.0	7.0 ± 0.9	7.1 ± 1.0	7.6 ± 0.7	0.58	0.633
Cup depth (cm)	11.7 ± 5.8	11.7 ± 4.9	16.3 ± 6.6	16.2 ± 4.8	2.45	0.074
Maximum water depth (cm)	9.7 ± 3.4	8.8 ± 3.5	10.2 ± 3.3	13.1 ± 2.1	2.61	0.061
Minimum water depth (cm)	1.3 ± 2.5	1.3 ± 3.0	0.8 ± 2.0	3.1 ± 2.6	1.01	0.397
Water depth (cm)	5.8 ± 3.1	5.6 ± 3.0	5.3 ± 2.5	9.3 ± 2.5	2.60	0.061

with standing water and the water levels of stumps were the most important factors influencing the breeding activity of *K. eiffingeri*. Bamboo stumps receive water solely from rain, and fluctuations of water levels of bamboo stumps were closely associated with rainfall patterns as predicted, i.e., water levels rose immediately on rainy days and gradually declined due to water loss by evaporation until the next rain. Our results suggest that water resources in the bamboo stumps are critical to the reproduction of *K. eiffingeri*, and the reproductive phenology is strongly dependent upon rainfall patterns. Hence, *K. eiffingeri* is an opportunistic species that breeds whenever an adequate amount of water is available in tree holes and bamboo stumps (Hsu et al. 2006).

It is interesting to note that the breeding activity of *K. eiffingeri* was dramatically reduced beginning on Aug. 21 even though water levels in the stumps remained high for another month, and air temperatures also stayed high in Aug. and Sept. compared to July. A similar result was also found in an earlier study in 2 bamboo forests at Chitou with similar temperature and moisture conditions (Kam et al. 1996). These findings suggest that factors other than water levels in the stumps and temperature are important in determining the end of the breeding season. One possibility is that *K. eiffingeri* exhibits physiological plasticity such that its endogenous reproductive cycle is synchronized with the annual cycle of local climatic conditions at Chitou to ensure the survival of offspring by decreasing the risk of desiccation. Desiccation is a major factor in tadpole mortality in temporary habitats (Smith 1983, Alford and Wilbur 1985, Wilbur 1987, Newman 1988, Laurila and Kujasalo 1999, Roedal et al. 2004). The larval period of *K. eiffingeri* tadpoles is 40-79 d depending on the brood size (Kam et al. 1998b). If a new egg clutch is oviposited in late summer, tadpoles may face habitat desiccation beginning in Oct. which is well before they reach the minimum size for metamorphosis. The other possibility is that *K. eiffingeri* is iteroparous, i.e., many females may have laid eggs in the early part of the season, and low energy reserves may prevent them from producing a 2nd clutch. Furthermore, tadpoles are obligatorily oophagous, and female frogs invest a tremendous amount of energy in provisioning offspring (Kam et al. 1997 1998b). If a new clutch of eggs is oviposited in late summer, female frogs may find it harder to obtain enough food to produce trophic eggs to feed the tadpoles in the fall when the dry season begins. Even if the tadpoles reach metamorphosis, the froglets would still face the harsh, dry, cold conditions of fall and winter (Wilbur and Collins 1973, Collins 1979).

Results showed that water in the bamboo stumps varied greatly, which is probably related to the characteristics of the stumps, their orientation, and spatial distribution (Kam et al. 1996, Kitching 2000, Roedel et al. 2004, Rudolf and Roedel 2005). Bamboo trees in our study site formed a fairly dense and uniform canopy, and the ground level consisted of annual herbs. A stepwise regression revealed that stump height and cup depth significantly influenced the water level fluctuations of stumps, which is a function of water received from rain and evaporative water loss. We contend that tall stumps could collect more rain because they are less covered by herbaceous plants on the forest floor compared to shorter stumps. On the other hand, most bamboo stumps are erect, receive direct sunlight for only a short period of time around noon, and the deeper the cup, the less sunlight there would be striking the water pool. Kitching (2000) reported that axil water in banana trees is more or less enclosed, which reduces evaporative losses. We contend that deep bamboo cups not only collect more water but have lower water evaporation compared to shallow bamboo cups. In addition, the spatial distribution of stumps may also affect water fluctuations; for example, field observations showed that bamboo cups located along the edge of habitats received considerably more sunlight, thus might have a higher rate of evaporative water loss (Kam per. obs.). Laessle (1961) reported that temperature, dissolved oxygen, carbon dioxide, and the pH of the water of bromeliad leaf axils fluctuated more in water of axils exposed to direct sunlight than those under a dense tree canopy.

Results of this study clearly showed that *K. eiffingeri* is selective about oviposition sites, which is probably related to the water resource in bamboo cups that varies greatly among stumps and is the most critical resource for the survival of their embryos and tadpoles (Kam et al. 1998a, Roedel et al. 2004). Frogs preferred stumps with deeper cups that contained more water, which may reduce the risk of desiccation in the case of a long interval between rain events. Earlier studies found that amphibians use water depth or the water-holding capacity of pools as a cue for oviposition site selection (Crump 1991, Spieler and Linsenmair 1997, Rudolf and Roedel 2005). We speculate that frogs also prefer taller stumps because the opening of the stumps are less likely to be covered by growing herbs as the season progresses so that they receive maximum rainfall (Kam et al. 1996).

Characteristics of stumps that were used 1, 2, 3, and 4 times did not significantly differ, suggesting that other factors determine the reuse of stumps. We propose that the frequency of stump use is correlated with the turnover rate of tadpoles in the stumps. In the beginning of the breeding season, all stumps are available for breeding pairs. After eggs are deposited in stumps, tadpoles hatch 10-14 d later and are confined in the pool until metamorphosis (Kam et al. 1998a). In this period, the stumps are probably not suitable for re-nesting because interclutch competition for food is severe between tadpoles in that size and the number of older tadpoles would have detrimental effects on the growth and development of younger tadpoles (Chen et al. 2001). However, as soon as the tadpoles metamorphose and leave, the stumps would again be available for reuse. Furthermore, earlier studies showed that egg and tadpole numbers varied among stumps, and the larval period is strongly dependent upon the initial brood size (Kam et al. 1996 1997). Tadpoles of *K. eiffingeri* are obligatorily oophagous (Ueda 1986); thus, growth, development, and survivorship of tadpoles are totally dependent upon trophic eggs provided by female frogs (Kam et al. 1997). Chen et al. (2001) experimentally demonstrated that the larval period varied among brood sizes. Tadpoles in smaller broods obtained relatively more trophic eggs from female frogs, grew and developed faster, and metamorphosed earlier than those in larger broods. Thus, once the stumps are tadpole-free, they are available for re-nesting.

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