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TIME- AND CONTEXT-DEPENDENT OVIPOSITION SITE SELECTION OF A PHYTOTELM-BREEDING FROG IN RELATION TO HABITAT CHARACTERISTICS AND CONSPECIFIC CUES

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ABSTRACT: Time- and context-dependent nest site selection of a phytotelm-breeding frog (*Kurixalus eiffingeri*) was evaluated in a natural bamboo habitat in subtropical Taiwan from 2004 to 2005. At the beginning of the breeding season (mid-March), frogs preferred bamboo stumps with large water holding capacity, which may be considered high-quality stumps since water availability is critical to the survival of tadpoles. Prior to 21 May, no tadpole-occupied stumps were re-used even though they represented 10–40% of total stumps at the study site; however, tadpole-occupied stumps were consistently re-used afterwards. Stumps with fewer tadpoles were used proportionally more than those with more tadpoles. By choosing the stumps with fewer tadpoles, the negative competitive effect of the late-clutch tadpoles on the early-clutch tadpoles would be somewhat alleviated. Male frogs did not breed in the same bamboo stump for consecutive breeding events, which may relate to the male reproductive strategy. We propose that it would often be a better strategy for a male frog to breed in different stumps than to stay in the same stump, even if the stump was of high quality. Breeding in multiple stumps would increase the number of breeding opportunities by reducing the interval between successive mating attempts, minimize the inter-clutch competition between tadpoles, and avoid competition between two cohorts of its own genetically-related tadpoles. Our results suggest that stump quality is indicated by water holding capacity and the number of the tadpoles in the stump during early and late breeding seasons. Thus, oviposition site choice in this species is dependent on stump quality, but stump quality is both context- and time-dependent.

Key words: Anura; Conspecific attraction; Desiccation risk; Nest-site selection; Phytotelmata

In oviparous organisms, breeding site selection is a crucial component of fitness. Adults have been shown to discriminate among potential breeding sites on the basis of a number of variables. For example, the presence or density of predators at breeding sites has frequently been associated with oviposition avoidance (Jowers and Downie, 2005; Kats and Sih, 1992; Murphy, 2003a; Petranka et al., 1994; Resetarits and Wilbur, 1989). Some studies have also found a negative relationship between the density of conspecifics and oviposition-site preference (Crump, 1991; Murphy, 2003a; Resetarits and Wilbur, 1989; Spieler and Linsenmair, 1997). Presumably, this preference is due to intra-specific competition and the resulting decreasing fitness at higher densities. Other studies, however, have suggested that individuals are attracted to breeding habitats with a high density of conspecifics because density serves as a reliable indicator of habitat quality (Muller et al., 1997; Rudolf and Rödel, 2005; Stamps, 1988).

In species with complex life cycles, it is also important that the permanence of the breeding habitat exceeds the total length of the larval period (Edgerly et al., 1998; Murphy, 2003b; Rudolf and Rödel, 2005). In more ephemeral habitats, desiccation is often a major source of larval mortality (Newman, 1988; Smith, 1983). Some studies have shown that adults can discern future habitat permanence and make oviposition decisions that minimize the risk to their offspring (Crump, 1991; Rudolf and Rödel, 2005; Spieler and Linsenmair, 1997). Since breeding habitats may deteriorate in quality over time or dry up entirely, cues that indicate the likely permanence of a habitat can also be important to breeding site choice. However, oviposition decisions can be time-dependent. Edgerly et al. (1998) found that oviposition strategies in female tree-hole breeding mosquitoes differed depending on the time of year, with females avoiding treeholes with conspecifics early in the season and seeking them out late in the season.

A number of studies have shown the importance of competition, predation or habitat

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413

permanence to oviposition site selection by varying one of these factors in oviposition choice experiments (Edgerly et al., 1998; Murphy, 2003a; Resetarits and Wilbur, 1989). However, in natural environments, individuals are often faced with multiple risk factors simultaneously when making oviposition decisions. In addition, the available information concerning risk factors varies temporally and spatially (Doligez et al., 2002). Relatively few studies have assessed how breeding site choices are made in these more complex scenarios with multiple risk factors. Using a tree-hole-breeding frog, Rudolf and Rödel (2005) provided some of the first evidence that oviposition site selection is context dependent (i.e., the relative importance of a single variable depends on the influence of other variables; see also Murphy, 2003a,b).

Phytotelmata have been used as microcosms to study oviposition site choice in a number of species (Kitching, 2000; Lehtinen et al., 2004; Srivastava et al., 2004). For example, arboreal pools (tree holes, bamboo stumps, leaf axils, and other such sites) are structurally simple microhabitats that occur on a small spatial scale. Thus, these microhabitats can be manipulated and monitored easily (e.g., Kam et al., 1996; Laessle, 1961; Rödel et al., 2004; Srivastava et al., 2004). Typically, these small water bodies receive only rain water, and water levels often fluctuate greatly depending upon the balance between evaporation and rainfall (Lin and Kam, 2008). In addition, while many arboreal pools are predator-free, they are also often food-limited (Laessle, 1961; Wassersug et al., 1981). In such conditions, competition for food is severe, and priority effects are obvious within and between species (Caldwell, 1993, Chen et al., 2001; Kam et al., 2001). Arboreal pools also differ physically and occur at low densities in most systems; thus, the quality and availability of these reproductive resources vary in time and space. Furthermore, as the reproductive season progresses, more and more of the limited number of arboreal pools may already have been used for breeding by other individuals (Heying, 2004). The presence of conspecifics in the arboreal pools could lower the quality of the breeding site due to intra-specific competition, which could affect oviposition site choice.

In this study, we used a Taiwanese frog (Kurixalus eiffingeri, Anura, Rhacophoridae) that breeds in water-filled bamboo stumps as a model animal to study the factors influencing breeding site choice. Specifically, we hypothesized that water permanence and competition for food among conspecific tadpoles would be important to oviposition site selection in this species. Based on this hypothesis, we predicted that frogs would choose bamboo stumps that were likely to retain water and avoid breeding in stumps with conspecific tadpoles. However, this choice may be context dependent. As more and more of the stumps are used and occupied by tadpoles, we predicted that bamboo stumps with conspecifics would be re-used later in the breeding season.

MATERIALS AND METHODS

Study Animal

Kurixalus eiffingeri is a small frog (SVL about 30–40 mm), endemic to Taiwan and two adjacent small islands, Iriomote and Ishigaki (Kuramoto, 1973; Ueda, 1986). During the breeding season (February–August), male frogs occupy bamboo stumps with standing water and call at night from the opening of the stumps to attract female frogs. Females in amplectant pairs then lay fertilized eggs above the water line on the inner walls of bamboo stumps (Kam et al., 1998a; Kuramoto, 1973). 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 embryos have hatched. Tadpoles are obligatorily oophagous and are fed by females that lay unfertilized, trophic eggs directly in the water in the absence of male frogs (Ueda, 1986). Female frogs visit and feed tadpoles at intervals of about 8 d, and feeding occurs only at night (Kam et al., 2000). Tadpoles are not cannibalistic, but interclutch competition for food is severe between tadpoles in that the size and number of older tadpoles can have detrimental effects on the growth and development of the younger tadpoles (Chen et al., 2001; Kam et al., 2001). The length of the larval period,

from hatching to metamorphosis, is approximately 50 d (Kam et al., 1998*b*). The pools of water in bamboo stumps also contain microorganisms (euglenoids, diatoms, paramecia, *Chlorella*, and rotifers) and the larvae of invertebrates (Culicidae, Chironomidae, and Tipulidae: Order Diptera) (C. F. Lin, 1996, unpublished data). The other species in the pools do not appear to have direct interactions with the tadpoles as they are neither food for nor the predators of the tadpoles, and they do not compete with tadpoles for trophic eggs (Kam et al., 1996; Ueda, 1986).

Study Site

We conducted experiments 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, Taiwan. We selected a 20 m × 40 m plot and marked every bamboo stump before the breeding season. The plot was divided into 128 grids using a 2.5 m × 2.5 m grid system, and the position of every stump was located. Three sides of the plot were surrounded by broad-leaf forests, and the remaining side was separated from other bamboo forests by a 6-m unpaved road. Bamboo formed a fairly dense canopy (12 m or higher), and herbs and a few shrubs were found on the ground level.

Field Surveys and Behavioral Observations

We visited the bamboo forest once a week from February 2004 to March 2005. We conducted direct sampling using transect methods on the study plot during the night time (1800–0200 h) where we checked the forest floor and every stump. The sequence in which stumps were sampled was randomly selected each night. We recorded any behavior (calling, wrestling, amplexus, egg-guarding, egg-feeding, etc.) of the frogs that we encountered. We recorded egg-guarding behavior when we observed male frogs either defending egg clutches against predators or brooding eggs (Chen et al., 2007). After behavioral observations, we captured and toe-clipped the frogs, and recorded the sex and capture location. Adult male frogs were identified by the presence of vocal sacs and/or nuptial pads.

Measurements and Monitoring of Oviposition Site Characteristics

Once a newly-laid clutch was found, we recorded the clutch size and developmental stage of the embryos following Gosner (1960). The following day, we measured the oviposition site characteristics of stumps which received a new egg clutch. Because the developmental time for eggs to hatch was 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, and (3) cup depth. Some stumps were never used by frogs; we measured the site characteristics of these stumps at the end of breeding season.

Because the water level of each stump fluctuated throughout the study period, we counted the number of stumps with standing water and measured the water depth in every stump weekly. We averaged the water depth, number of weeks with standing water, and maximum and minimum water depth of all stumps in the study plot. In addition, we averaged the coefficient of variation (CV) of water depth of all stumps after the CV of water depth of each stump was determined.

Each week, we also monitored the eggs and tadpoles in every stump. If eggs were freshly-deposited, we measured the clutch size. After hatching, we continued to monitor the tadpole number weekly until no tadpoles were left in the stumps. To facilitate the examination and measurement of tadpoles, on our first visit we made a V-shaped cut in each bamboo stump and detached the portion of the stump containing the water and tadpoles. This allowed us to easily pour out the water and tadpoles. After data collection, the water and tadpoles were placed back in the detached portion of the stump, which was then placed in the V-shaped notch in the basal part of the stump. The detached portion fit snugly in the notch, and transparent tape was wrapped around the cut for additional support. Because female frogs feed their tadpoles at night (Kam et al., 2000), we examined the bamboo stumps during the day to minimize disturbance of maternal feeding behavior.

TABLE 1.—Physical conditions of used (once- and re-used stumps) and unused stumps. Values are means ± SD. Numbers in parentheses = n. See the materials and methods section for definitions of used, unused, once-used, and re-used stumps.

Variables	Total used stumps (57)	Once-used (38)	Re-used (19)	Unused stumps (44)
Trunk height (cm)	40.22 ± 15.06	38.89 ± 16.75	42.87 ± 10.87	30.91 ± 12.28
Stump diameter (cm)	7.14 ± 0.96	7.19 ± 1.00	7.04 ± 0.90	6.88 ± 1.28
Cup depth (cm)	12.53 ± 5.61	12.16 ± 5.69	14.41 ± 5.89	8.22 ± 5.01
Maximal water depth (cm)	9.84 ± 3.46	9.56 ± 3.42	10.39 ± 3.56	5.49 ± 3.05
Minimal water depth (cm)	1.43 ± 2.58	0.99 ± 2.13	2.29 ± 3.18	0.24 ± 1.05
Mean water depth (cm)	6.17 ± 3.09	5.90 ± 2.86	6.69 ± 3.52	2.18 ± 2.17
Coefficient of variation of water level (%)	49.52 ± 25.09	50.91 ± 22.14	47.65 ± 30.62	143.98 ± 84.50
Number of weeks with standing water (wk)	23.63 ± 3.90	23.03 ± 3.96	24.84 ± 3.59	12.41 ± 8.42

Statistical Analyses

"Used stumps" were defined as stumps that were used by frogs to deposit fertilized eggs, which included stumps that were used once (referred to as "once-used" hereafter) or more than once (referred to as "re-used" hereafter). "Re-used stumps" were those where a new clutch of fertilized eggs were laid on the inner wall of stump above the water line when tadpoles from the previous clutch were present in the water pool (Kam et al., 1997). Oviposition site variables were compared between used and unused stumps, re-used and unused stumps, and re-used and once-used stumps using ANOVA, and the significance level was adjusted using the sequential Bonferroni method to correct for multiple comparisons (Rice, 1989). Variables were either log transformed (cup depth and water depth) or square-root transformed (maximal and minimal water depth) to meet the assumption of normality.

We used multiple logistic regression (SPSS for Windows, version 13.0) to analyze the importance of abiotic variables for the selection of oviposition sites. We did three multiple logistic regression analyses, one comparing total used and unused stumps, one comparing re-used and unused stumps, and one comparing once-used and re-used stumps. These analyses included eight habitat variables (Table 1). To ensure the independence of these predictor variables, we calculated the correlation coefficients among these variables and excluded one when correlation coefficients exceeded 0.7. Pearson χ^2 values and Hosmer and Lemeshow tests were used to assess the overall goodness-of-fit of the model, and a 2 × 2 classification table was used to assess the predictive performance of the model Nagelkerke (R^2_N) and Cox and Snell R^2 values were used to assess the amount of variation explained by the model. Significant habitat variables were assessed using Wald values.

RESULTS

We marked 101 stumps in the study plot, and 56% of the available stumps (57/101) were used as oviposition sites (Table 1). We captured 373 individuals and marked 89 males and 38 females; many individuals were captured repeatedly during the 13-mo study period. The majority of the frogs were observed between March and August.

The first egg clutch was found on 13 March, and tadpoles were first observed on 27 March (Fig. 1). From March to May, stump occupancy increased, reaching 40% by 8 May. However, during this period, new egg clutches were always deposited in unoccupied stumps (except one case in April). ANOVA results indicated that all variables were significantly different between used and unused stumps except stump diameter (Table 1). In the logistic regression analysis of used and unused stumps, we excluded maximum water depth and CV of water depth as these variables were highly correlated with others. The logistic regression model was a significant predictor of stump use (χ^2 = 67.11, df = 6, P < 0.0001) and included only one variable: number of weeks with water (Table 2). Number of weeks with water was positively correlated with probability of stump use, indicating a preference for oviposition sites with a longer hydroperiod. The model explained a relatively large amount of the variation in stump use (R^2_N = 0.65) and had high predictive performance
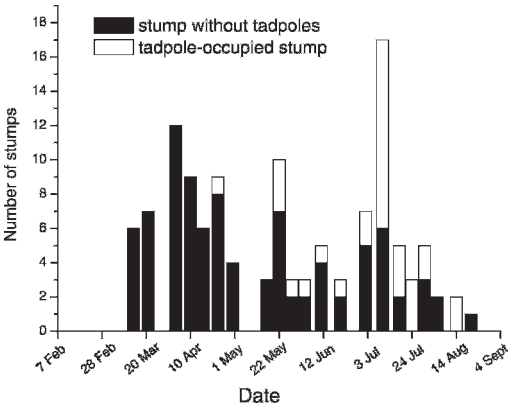
FIG. 1.—Number of egg clutches found in stumps from February 2004 to September 2004. Open bars indicate the number of egg clutches found in stumps that were used previously by females for oviposition.

(83.2%), indicating that the model could discriminate between used and unused stumps well.

After peak stump usage on 8 May, 20–30% of oviposition events occurred in tadpole-occupied stumps, even though there were many unoccupied stumps available for oviposition. Re-use of tadpole-occupied stumps occurred even more frequently in July and August when often more than 50% of oviposition events occurred in tadpole-occupied stumps (Fig. 2). When the characteristics of re-used and unused stumps were compared using ANOVA, results again indicated that all stump variables were significantly different except stump diameter (Table 1). In the logistic regression analysis of re-used and unused stumps, we excluded mean, maximum and CV of water depth as these variables were

highly correlated with others. The logistic regression model was a significant predictor of stump use (χ^2 = 48.645, df = 5, P < 0.0001) and included three variables: stump height, cup depth, and number of weeks with water (Table 2). All three variables were positively correlated with probability of stump use, indicating a preference for oviposition site with a taller stump, deeper cup, and longer hydroperiod in the stumps. The model again explained a relatively high amount of the variation in stump use (R^2_N = 0.76) and had high predictive performance (88.9%), indicating that the model could discriminate between the re-used and unused stumps well.

In the second half of breeding season, many stumps have already contained tadpoles, but many of them were re-used. ANOVA comparisons between once-used and re-used stumps indicated that no variables were significantly different (Table 1). In the logistic regression analysis of once-used and re-used stumps, we excluded mean and maximum water depth as these variables were highly correlated with others. The logistic regression model was unable to statistically distinguish between once-used and re-used stumps (χ^2 = 8.969, df = 6, P = 0.175, R^2_N = 0.202).

When we found that a stump was re-used, we compared the tadpole number in this stump to that in the nearest used stumps. We found that the number of tadpoles in the re-used stumps (10.85 $\pm$ 13.31 tadpoles, n = 27) was significantly fewer than that of once-used stumps (22.86 $\pm$ 19.02 tadpoles, n = 27, t = 2.65, df = 52, P = 0.017). A Kolmogorov

TABLE 2.—Significant stump parameters (out of eight) in the logistic regression analyses comparing total used (n = 57) and unused stumps (n = 44) and re-used (n = 19) and unused stumps (n = 44). *B is regression coefficient. SE is the standard error of the regression coefficient; The Wald statistic is used to evaluate the significance of a variable in predicting stump use.

Variables	*B	SE	Wald	df	P
Total used vs. Unused[a]					
Weeks with water	0.206	0.067	9.524	1	0.002
Re-used vs. Unused[b]					
Stump height	0.125	0.056	4.979	1	0.026
Cup depth	0.370	0.150	6.068	1	0.014
Weeks with water	0.373	0.130	8.171	1	0.004

[a] Cox & Snell R^2 = 0.485; Nagelkerke R^2_N = 0.651
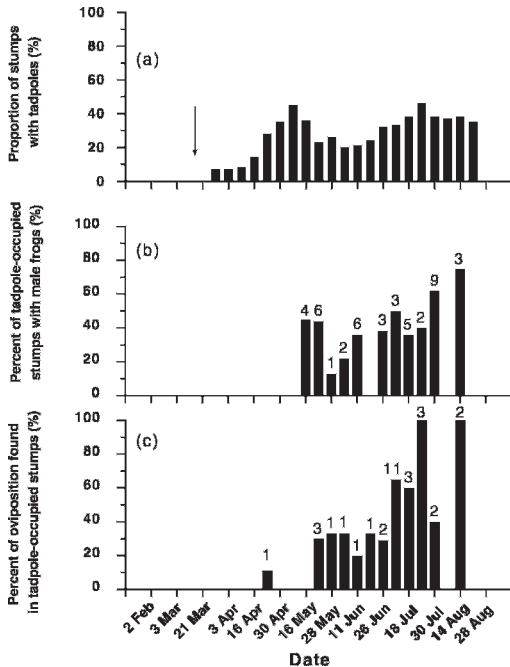[b] Cox & Snell R^2 = 0.538; Nagelkerke R^2_N = 0.762

FIG. 2.—Weekly survey of (a) the tadpole-occupied stumps in the study plot, (b) proportion of these stumps occupied by male frogs, and (c) the proportion re-used for oviposition. Numbers above the bars in (b) and (c) represent the total number of male frogs and re-oviposition events, respectively. An arrow in (a) represents the initial of breeding season.
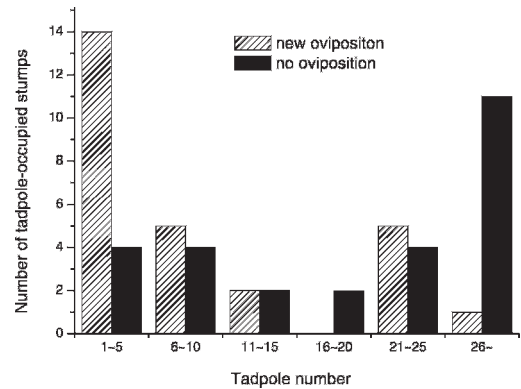

FIG. 3.—The number of tadpoles in tadpole-occupied stumps that were found with new oviposition compared with the nearest tadpole-occupied stump with no new oviposition. $n = 27$.

Goodness-of-Fit test also revealed that the frequency distribution of the tadpole number of re-used and once-used stumps were statistically different ($D = 0.374$, $P = 0.049$; Fig. 3).

We monitored the movement of marked male frogs and found that they never stayed in the same stump after a breeding event (average movement distance 12.28 ± 7.22 m, range: 1.5–30 m, $n = 39$). No male frogs were found to use the same stump for consecutive breeding events. The average distance between the two stumps used for breeding by an individual male frog was 13.85 ± 7.56 m (range; 2.75–30 m, $n = 20$).

DISCUSSION

While arboreal pools offer some advantages as oviposition sites (e.g., absence of predators and interspecific competition), they are also prone to desiccation (Rudolf and Rödel, 2005; Srivastave et al., 2004). Thus, water availability is critical to the survival of offspring. *Kurixalus eiffingeri* selected oviposition sites so as to reduce the risk of desiccation for tadpoles during the larval period (Lin and Kam, 2008). Results from comparing used and unused stumps suggest that frogs prefer stumps with large water holding capacity, which may be considered high quality stumps. Low quality stumps (those with low water holding capacity) were never used. Since stumps vary in physical characteristics and water-holding capacity, it is not surprising to see that only 56% of the total stumps were used by frogs (Lin and Kam, 2008).

Prior to 21 May, no tadpole-occupied stumps were re-used even though they represented 10–40% of total stumps at the study site. This result suggests that frogs initially avoid ovipositing in tadpole-occupied stumps. Similar behavior has been reported in *Hyla pseudopuma* and *Pleurodema borellii* in that adult frogs avoided using water bodies with conspecific tadpoles as breeding sites (Crump, 1991; Halloy and Fiano, 2000). Earlier studies on *K. eiffingeri* have shown severe inter-clutch competition between successive cohorts of tadpoles. Older tadpoles outcompete younger tadpoles for trophic eggs and suppress their growth and development (Chen et al., 2001; Kam et al., 1997). Thus, *K. eiffingeri* that lay fertilized eggs in unoccupied stumps would avoid inter-clutch competition, which in turn increases survival and the probability of metamorphic success.

Repeated use of stumps by frogs, which occurred only later in the breeding season, can be viewed as a tradeoff between poor stump quality and inter-clutch competition among tadpoles. As the breeding season began, frogs chose arboreal pools with large water-holding capacity. However, as more and more stumps were used, unoccupied but good quality stumps were no longer available. At this point, frogs have two choices: they either use tadpole-occupied stumps whose quality is discounted due to the presence of tadpoles or use available unoccupied stumps whose overall quality is inferior.

One explanation for the re-use of stumps is that even though the quality of tadpole-occupied stumps is discounted, they are still as good as, if not better than, the remaining unoccupied stumps. For frogs that lay eggs in the tadpole-occupied stumps, their offspring may be competitively inferior to the tadpoles existing in the pools (i.e., early-clutch tadpoles), and their growth and development may be depressed (Chen et al., 2001). However, the presence of early-clutch tadpoles may represent the high quality of the stumps, i.e., the availability and persistence of the water resource. Similar findings of conspecific attraction have been reported in vertebrates and invertebrates (Doligez et al., 2002; Mokany and Shine, 2003; Rudolf and Rödel, 2005; Stamps, 1988). Thus, instead of using the unoccupied stumps where the water resources are unpredictable, frogs may prefer the more predictable but tadpole-occupied stumps.

In this study, stumps with fewer tadpoles were used proportionally more than those with more tadpoles. Kam et al. (1997) reported that new clutches of fertilized eggs were laid in occupied pools only when tadpole density was low, from 2–5 tadpoles. By choosing stumps with fewer tadpoles, the negative effect of early-clutch tadpoles on late-clutch tadpoles would be somewhat alleviated, since an increased number of early-clutch tadpoles in the pools could cause total mortality of late-clutch tadpoles (Chen et al., 2001). Furthermore, to choose occupied stumps with few but large tadpoles is likely the better strategy since these tadpoles will soon metamorphose, minimizing inter-clutch competition (Chen et al., 2001).

Male frogs did not breed in the same bamboo stump for consecutive breeding events, which may relate to the male reproductive strategy. For phytotelm-breeding frogs, high quality breeding sites are always limited (Kam et al., 1996; Heying, 2004), and in theory, it may be selectively advantageous for male frogs to occupy the same high-quality stump throughout the breeding season. Male frogs may breed repeatedly either with or without overlapping cohorts, and in either case incur a cost. In the latter case, occurrence of tadpoles of two cohorts is separated temporally, thus interclutch competition is avoided. However, given that the average larval period is about 50 d, a male frog would have to wait for a long time before having another chance at reproduction (Kam et al., 1997, 1998b), which may greatly reduce the number of breeding opportunities for a male frog within a breeding season. In contrast, if male frogs breed with overlapping cohorts, they may reduce the time interval between successive breeding attempts and be able to rapidly produce multiple clutches within a breeding season. However, tadpole competition between cohorts of its own offspring is unavoidable, and tadpole survival is greatly reduced. We propose that for a male frog to breed in different stumps with fewer tadpoles would often be a better strategy than staying in the same stump. This strategy would increase the number of breeding opportunities by reducing the interval between successive mating attempts, minimize the inter-clutch competition between tadpoles, and avoid competition between two cohorts of genetically related tadpoles.

In summary, our results documented the reproductive strategy of male phytotelm-breeding frogs: at the beginning of breeding season, male frogs choose breeding sites based on the physical characteristic of stumps where stumps that hold more water are preferred. After a male frog successfully mates, he stays in the stump to guard the embryos until they hatch. As soon as the embryos hatch, the male leaves the stump and searches for a new stump to initiate the next breeding event. However, as more and more stumps are used as the breeding season progresses, the male frog has fewer unoccupied stumps to choose

from. The male frog could choose either an empty stump of lower quality or a tadpole-occupied stump with inter-clutch competition. Our results suggest that males prefer a tadpole-occupied stump with fewer, more developmentally advanced tadpoles. We contend that the presence of tadpoles represents the quality of the stump, and by choosing stumps with fewer tadpoles, male frogs could not only obtain a good-quality stump but also avoid prolonged inter-clutch competition for their offspring.

Our results also suggest that when unoccupied breeding sites are abundant at the beginning of the breeding season, stump quality is indicated by water holding capacity. Later in the breeding season, when unoccupied high-quality sites are limited, quality is indicated by the number of tadpoles in the stump. Thus, oviposition site choice in this species is dependent on stump quality but stump quality is both context- and time-dependent.

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