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Testing the Nest-Homing Abilities of a Phytotelm-breeding Frog, *Chirixalus eiffingeri* (Rhacophoridae)

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We conducted a manipulative experiment to assess the homing of female *Chirixalus eiffingeri* to the nest. There were three experimental treatments and a control. For the control treatment, bamboo stumps were cut off at the base and reattached. In the first experimental treatment, when stumps were displaced 1 m, the proportion of stumps attended by females and the growth of tadpoles did not differ from the results of the control treatment, suggesting the 1-m stump displacement did not affect the nest homing of female frogs. In the second experimental treatment, when a bamboo stump was displaced 1 m and a new bamboo stump with tadpoles was put in its place, some females fed tadpoles in the displaced stump (3/12), but some fed tadpoles in the stump (3/12) at the original site. This finding suggests that the addition of a new stump confused the female frogs spatially, which resulted in females feeding the tadpoles in either stump. In the third experimental treatment, when a bamboo stump was displaced 1 m and a new stump without tadpoles was added at the original site, some female frogs fed tadpoles in the displaced stump (5/12) but some laid trophic eggs in the stump (4/12) at the original site, also indicating the female frogs were confused spatially. The overall results support the hypothesis that females rely on the spatial distribution of a nest stump, relative to other bamboo stumps, for nest homing to feed their offspring, and that stump location is an important cue to the nest homing of females.

Key words: anuran, *Chirixalus eiffingeri*, homing, oophagous tadpoles, phytotelmata

INTRODUCTION

Deposition of eggs on arboreal microhabitats is a unique reproductive mode among anuran species (Duellman and Trueb, 1986). To date, at least 102 species in 44 genera and 9 families are known to use arboreal microhabitats, or phytotelmata, for reproductive activities (Lehtinen *et al*., 2004). These phytotelmata are small pools of water that can be found in leaf axils, flowers, tree holes, bamboo stumps, snail shells, and nut capsules (Duellman and Trueb, 1986; Lannoo *et al*., 1987; Summers, 1990; Caldwell, 1993; Kam *et al*., 1996; Rudolf and RÖdel, 2005). Due to limited food in the phytotelms, maternal provisioning by feeding fertilized or unfertilized eggs to arboreal tadpoles has evolved in at least 10 anuran species (Weygoldt, 1980, 1987; Ueda, 1986; Lannoo *et al*., 1987; Caldwell, 1997; Lehtinen *et al*., 2004). Female frogs usually return to the nests to feed the tadpoles every 4 to 8 days (Brust, 1993; Jungfer, 1996; Thompson, 1996; Caldwell and de Oliveira, 1999; Jungfer and Weygoldt, 1999; Kam *et al*., 2000).

The ability of female frogs to home precisely to their nest during each visit is critical for the survival of obligatorily oophagous tadpoles and helps the females avoid feeding genetically unrelated tadpoles. However, the mechanism by which female frogs home to provision their tadpoles is largely unstudied. Adult *Dendrobates pumilio* are able to return to their home areas following experimental displacements (McVey *et al*., 1981), probably using, in part, airborne olfactory cues from plants (Forester and Wisnieski, 1991). Brust (1990) described the nest searching behavior of *D. pumilio* and noted that female frogs sometimes explore the axil containing their young and other plant axils before or after feeding their tadpoles. Furthermore, between provisioning events females occasionally investigate axils without depositing eggs. Chiu and Kam (2006) conducted a series of manipulative experiments to assess the nest homing of a rhacophorid (*Chirixalus eiffingeri)*, and the results suggested that the location of stumps is the most critical cue in nest homing of females of that species. They further hypothesized that females rely on the spatial distribution of the nest stump relative to other bamboo stumps for nest homing to feed their offspring.

In this study, we conducted manipulative field experiments by displacing nests and adding stumps to further examine the mechanism of homing proposed by Chiu and Kam (2006). Specifically, if the spatial distribution of the nest stump relative to other bamboo stumps is critical to the nest homing of the female frogs, then we would expect the homing to be affected if a stump is added around the nest.

MATERIALS AND METHODS

Study site and animals

We conducted a manipulative experiment in bamboo forests of the Experimental Forest of National Taiwan University at Chitou, which was described elsewhere (Kam *et al*., 2000). Briefly, Chitou

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has a distinct wet and dry season, and the annual mean air temperature is about 17°C (12–22°C). *Phyllostachys edulis* and *Sinocalamus latiflorus* are the most abundant plants at the study site (Kam *et al.*, 1996). The bamboo is cut periodically for commercial purposes, and the stumps collect rain water and become ideal nesting sites for *C. eiffingeri* (Kam *et al.*, 1996). *Chirixalus eiffingeri* breeds from February to August, and females lay fertilized eggs on the inner walls of bamboo stumps above the water surface (Kuramoto, 1973; Kam *et al.*, 1998a). Tadpoles are obligatorily oophagous and are fed by females, who lay unfertilized eggs in response to the "egg-begging" behavior of the tadpoles (Ueda, 1986). The tadpole period is about 50–60 d (Kam *et al.*, 1998b).

Experimental protocol and ethical considerations

We conducted the experiment from March to August 2003. We located 50 bamboo stumps containing tadpoles that were about 2 weeks old and in the early stage of development (Gosner stage 26–28; Gosner, 1960). We randomly assigned 14 stumps to a control treatment and 12 stumps each to three experimental treatments. Bamboo stumps in the control treatment were sham-treated. The stumps were cut off at the base and secured with iron rods and wire at the original site (Table 1). In the first experimental treatment (called the No Stump or NS treatment), each bamboo stump was sawn off at the base, moved 1 m in a randomly selected direction from its original location, and secured with iron rods and wire (Table 1). In the second experimental treatment (called Added Stump and Tadpole or AS+T treatment), each bamboo stump was sawn off at the base and displaced 1 m (AS+T$_{out}$ stump) in a randomly selected direction. We then put a new bamboo stump, containing tadpoles (AS+T$_{in}$ stump) collected elsewhere, on the original site of the displaced stump (Table 1). In the third experimental treatment (called Added Stump or AS treatment), the bamboo stumps were sawn off at the base and displaced 1 m (AS$_{out}$ stumps) in a randomly selected direction. We then placed a new bamboo stump without tadpoles (AS$_{in}$ stumps) on the original site of each displaced stump (Table 1).

Each pair of an added and displaced stump was similar in size, shape, and coloration. The added stumps (AS$_{in}$ or AS+T$_{in}$ stumps) were collected from other areas in the bamboo forests and did not contain tadpoles when cut. All tadpoles in stumps (control, NS, AS$_{out}$, and AS+T$_{out}$ stumps) were removed and replaced by 10 tadpoles that had been collected from different bamboo forests. We also added 10 tadpoles into the AS+T$_{in}$ stumps. Water in the stumps was removed and replaced by about 250 ml of rainwater (Kam *et al.*, 2001). We maintained the water volume in each bamboo stump by adding rainwater or removing excess water as needed. These procedures were designed to minimize variation in the water content of the stumps.

In this study, we displaced bamboo stumps to study nest homing. Unlike most earlier studies (Dole, 1968; McVey *et al.*, 1981; Crump, 1986), this study did not involve the displacement of female frogs or the direct observation of the homing of female frogs. This was because the nest homing of *C. eiffingeri* females to feed their tadpoles takes place at night at an interval of 6–14 days (Kam *et al.*, 2000; Kam and Yang, 2002), and feeding behavior is sensitive to disturbances, such as the movements of researchers and illumination from flashlights (Chiu and Kam, 2006). Thus, the handling of frogs, including capture and displacement, affects their nest homing behavior. Instead of displacing female frogs, we displaced bamboo stumps (*i.e.*, nests), which can be cut and displaced easily. The advantage of displacing stumps is that female frogs remain undisturbed. In this study, we only used those tadpole-occupied stumps that were at least five m away from the nearest tadpole-occupied stump. We did this because the average activity range of female frogs during the breeding season is about 12.9 m^2; if this range were circular, its radius would be about 2 m (K.-S. Chuang, unpublished data). Thus, if the tadpoles in the stumps were fed during the experiments, they would most likely be fed by the same female frog.

Experimental procedures were described in detailed in an earlier study (Chiu and Kam, 2006). Briefly, we assessed the return of female *C. eiffingeri* to the nest by monitoring the feeding status (*i.e.*, presence of trophic eggs in the stomach) and growth of tadpoles weekly. We conducted all experiments for a two-week period to minimize the stress of starvation on any tadpoles that were not fed during the experiments. *Chirixalus eiffingeri* tadpoles are obligatorily

Table 1. Experimental design and the results of tadpole feeding in the control, NS, S, and S+T treatments.

	Original site	Displaced 1-m
Control treatment (*n*=14)	Tadpoles of 9 stumps (C1-2, C4, C7-10, C12-13) were fed both weeks	No stump at this location
NS treatment (*n*=12)	No stump at the original site	Tadpoles in 8 stumps (NS1-3, NS5, NS7, NS10-12) were fed both weeks
AS+T treatment	**AS+T$_{in}$ stumps (*n*=12)** Tadpoles in 3 stumps (AST4, AST5, and AST10) were fed both weeks	**AS + T$_{out}$ stumps (*n*=12)** Tadpoles in 3 stumps (AST3, AST6, and AST9) were fed both weeks
AS treatment	**AS$_{in}$ stumps (*n*=12)** Trophic eggs were found in AS8 and AS10-12 during the first week	**AS$_{out}$ stumps (*n*=12)** Tadpoles in 3 stumps (AS1, AS3, and AS5) were fed both weeks Tadpoles in 2 stumps (AS8 and AS11) were fed during the second week

Bamboo stumps in the control treatment were sham-treated, *i.e.*, stumps were cut off at the base and secured at the original site). The NS, AS+T$_{out}$, and AS$_{out}$, stumps were displaced 1 -m. In the first experimental treatment (called No Stump or NS treatment), no stump was added at the original site. In the second experiment group (called Added Stump and Tadpole or AS+T treatment), a new stump with tadpoles (AS+T$_{in}$) was put on the original site of each displaced stump (AS+T$_{out}$). In the third experimental treatment (called Added Stump or AS treatment), a new stump (AS$_{in}$) without tadpoles was put on the original site of each displaced stump (AS$_{out}$). The control treatment had 14 replicates (which labeled C1-14), whereas the NS, AS+T, and AS treatments had 12 replicates each, labeled (NS1-12, AST1-12, and AS1-12, respectively). For the AS+T and AS treatments, each replicate consisted of two bamboo stumps, one was a displaced stump and the other was the new stump that was placed on the original site of each displaced stump.

oophagous (Kam *et al.*, 1996); thus, their feeding status and growth are reasonable assessments of female nest homing (Kam *et al.*, 2000). We defined fed tadpoles as those with jelly capsules in their pool and/or eggs in their stomach. Unfed tadpoles lacked jelly capsules in their pool and eggs in their stomach. While conducting the experiments, we adhered to the guidelines for the use of animals in research and the legal requirements of the National Science Council, Taiwan, R.O.C.

Statistical analyses

Each stump was considered an experimental unit, and data were analyzed with SAS (SAS Institute, Inc., 1996). We used the chi-square test to determine whether the frequency of fed or unfed nests was independent of treatment. Each treatment mean was calculated from the mean of the total length (TL) of all tadpoles (fed and unfed) in each bamboo stump. We did not adjust the final TL of tadpoles because the initial TL of tadpoles between treatments in all experiments was statistically similar. After log-transforming the data to meet the parametric assumption of normality, we analyzed the growth pattern using a repeated-measure ANOVA, and used the sequential Bonferroni method for multiple comparisons (Rice, 1989). Unless stated otherwise, we report the mean±SD of each variable.

RESULTS

Tadpoles in 9 out of 14 stumps in the control treatment were fed, as were tadpoles in 8 NS, 5 AS_{out}, and 3 $AS+T_{out}$ stumps (out of 12 stumps per treatment). The number of stumps in which tadpoles were fed was independent of treatment (χ^2_3=5.809, *P*=0.121).

Overall, there were significant differences in the growth pattern of tadpoles among treatments (repeated measures ANOVA, $F_{3,46}$=11.22, *F*<0.0001; Fig. 1). Multiple comparisons showed that tadpole growth in the control treatment was significantly different from that of the AS_{out} and $AS+T_{out}$ stumps (repeated-measures ANOVA, $F_{1,24}$=20.75, *F* = 0.0001, $F_{1,24}$=10.46, *F*=0.003, respectively; Fig 1). In addition, tadpole growth in the NS treatment was significantly different from that of AS_{out} and $AS+T_{out}$ stumps (repeated measures ANOVA, $F_{1,22}$=24.71, *F*=0.0001, $F_{1,22}$=11.79, *F*=0.002, respectively ; Fig. 1).

In the AS+T treatment, we placed a new stump with tadpoles at the original site of each displaced stump to determine whether the addition of stumps and tadpoles affects the nest-homing behavior of the female frogs. We found that when tadpoles in an $AS+T_{in}$ stump were fed, the tadpoles in the corresponding $AS+T_{out}$ stump were not fed, and vice versa (Table 1). For example, tadpoles in three $AS+T_{in}$ stumps (AST 4, 5, and 10) were fed, but the tadpoles in the corresponding $AS+T_{out}$ stumps were not. Conversely, tadpoles in three $AS+T_{out}$ stumps (AST 3, 6, and 9) were fed, but the tadpoles in the corresponding $AS+T_{in}$ stumps were not.

In the AS treatment, we placed a new stump without tadpoles at the original site of each displaced stump to determine whether the addition of stumps alone affects the nest homing behavior of the female frogs. Although no tadpoles were present in the AS_{in} stumps, we were surprised to find trophic eggs in the water of four of them (AS 8, 10, 11, and 12 stumps) during the first week (Table 1). Trophic eggs are unfertilized eggs that are usually laid in a clutch in the water, whereas fertilized eggs are laid singly on the inner surface of bamboo stumps above the water line. In addition, there were two replicates (AS 8 and 11) in which trophic eggs were found in the AS_{in} stumps, and in which the tadpoles in the AS_{out} stumps were fed. However, these two events occurred at different times (Table 1). We found trophic eggs in the AS_{in} stumps during the first week, but the tadpoles in the corresponding AS_{out} stumps were not fed until the following week.

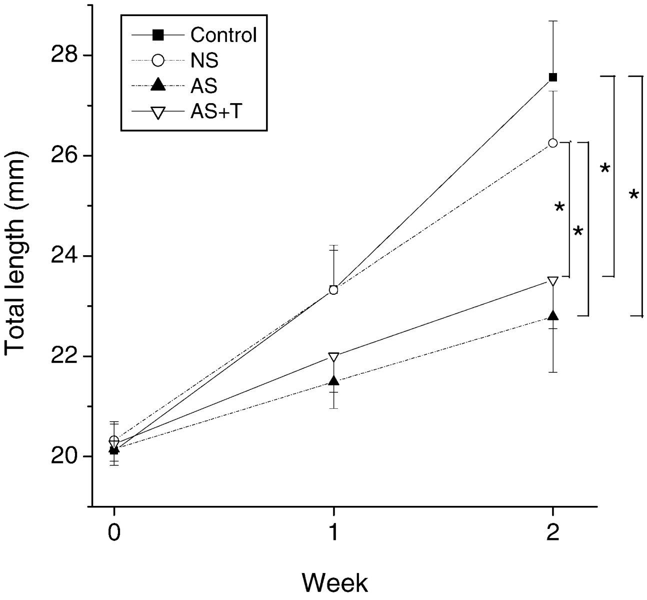

Fig. 1. *Mean (±SD) total length (TL) of tadpoles in the control and other treatments (NS, AS_{out}, and $AS+T_{out}$ stumps that were displaced 1 m). There were 14 stumps for the control treatment and 12 stumps for the other treatments. Each point is the average of the mean TL of all tadpoles (fed and unfed) in each bamboo stump. Multiple comparisons of tadpole growth between treatments were made with the sequential Bonferroni method, and the pairs compared that showed a statistically significant difference are labeled with "*". See Table 1 for a detailed description of the control and the three experimental treatments.

DISCUSSION

Clutch desertion by female *C. eiffingeri* is common (Kam *et al.*, 1997, 1998b), and the proportion of bamboo stumps deserted by female frogs in the control treatment of this study was similar to the proportion deserted during earlier studies conducted in the same region (Chen *et al.*, 2001). Based on our field observations (Kam *et al.*, 1997, 1998b; Chen *et al.*, 2001), most clutch desertion was caused by clutch abandonment or the death of female frogs.

In the NS treatment, when stumps were displaced 1 m, the proportion of stumps attended by females and the growth of tadpoles were not significantly different from the control treatment, suggesting the 1-m stump displacements did not affect the nest homing of female frogs. Chiu and Kam (2006) proposed that female frogs use the spatial distribution of their nest relative to other stumps as a homing cue, a case of landmarks as a cue for homing. A short displacement (*i.e.*, 1 m), such as in this study, probably does not alter the position or spatial distribution of a nest stump relative to other bamboo stumps sufficiently to prevent a female frog from returning to her brood (Sinsch, 1990, 1993;

Gonser and Woolbright, 1995). On the other hand, a longer displacement (*i.e.*, 3 m) does change the distribution of a nest stump relative to other bamboo stumps to such an extent that female frogs are no longer able to find their nests (Chiu and Kam, 2006).

In the AS+T treatment, when a bamboo stump was displaced 1 m and a new bamboo stump with tadpoles was put in its place, some females (3/12) fed tadpoles in the displaced stump (AS+T_{out} stumps), whereas others (3/12) fed tadpoles in the stump at the original site (AS+T_{in} stumps). This finding suggests that the addition of a new stump confused the female frogs spatially, which resulted in females feeding the tadpoles in either AS+T_{in} or AS+T_{out} stumps. We contend that the addition of a stump probably changes the spatial distribution of the nest stump relative to other bamboo stumps to such an extent that female frogs are no longer able to locate their nests. Supportive evidence reported by Chiu and Kam (2006) indicated that tadpoles that were added to an unoccupied stump located within 1 m of a tadpole-occupied stump were not fed. Weygoldt (1980) reported a similar finding in *D. pumilio* in which eight of the tadpoles placed in axils were not provided with eggs, even when other tadpoles were fed in the adjacent axils of the bromeliad.

The results of the AS+T treatment provide indirect yet important information on the possible mechanism of nest homing of female *C. eiffingeri*. In the AS+T treatment, female frogs fed tadpoles in either the AS+T_{out} or AS+T_{in} stumps, suggesting they were confused spatially. Furthermore, females that fed tadpoles in an AS+T_{out} stump during the first week fed them again the next week, similarly females that fed tadpoles in an AS+T_{in} stump during the first week fed them again the second week. Thus, female frogs were confused spatially during the first week, but they were able to return to the same brood during the second week, suggesting females acquire a new homing route after a brief spatial confusion.

Earlier studies have suggested that chemical cues are not important in nest homing of female *C. eiffingeri* (Chiu and Kam, 2006), and that for short-distance movements of nest homing, visual cues might be more effective than olfactory cues for locating nest sites precisely (Sinsch, 1992). However, the mechanism and process of acquiring a new homing route is still unclear. Brust (1990) reported a complex nest-searching behavior in *D. pumilio* in which, during offspring provisioning, females sometimes explored their young's axils and other plant axils before and/or after feeding their tadpoles; between provisioning events, females occasionally investigated axils containing offspring but did not deposit eggs again. The searching of axils after feeding young may not only help a female to acquire a homing route but also reinforce a female's ability to remember the location of her young versus the axils of other, unrelated tadpoles using topographic or olfactory cues (Forester, 1986; Brust, 1990; Forester and Wisnieski, 1991).

In the AS treatment, when a new stump without tadpoles (AS_{in}) was added, female frogs either fed tadpoles in AS_{out} stumps (*i.e.*, AS 1, 3, 5, 8, and 11) or laid trophic eggs in AS_{in} stumps (*i.e.*, AS 8, 10, 11, and 12), indicating that the females were confused spatially. Although female frogs laid trophic eggs in AS_{in} stumps where no tadpoles were present during the first week, they did not do so in the second week. During week two, females started to lay eggs in AS_{out} stumps (AS 8 and 11). We hypothesize that the female frogs initially returned to the S_{in} stumps to lay eggs, but without the stimuli of tadpoles, began to search for a stump with tadpoles and eventually laid eggs in the AS_{out} stumps. Perhaps the egg-begging behavior of tadpoles plays an important role in maintaining the nest-homing ability of females (Kam and Yang, 2002). Even though we terminated our experiments after two weeks, we did check the AS_{in} stumps for two more weeks and found no trophic eggs laid in them.

In conclusion, our results support the contention that the location of stumps is the most critical cue in nest homing by *C. eiffingeri* females, and that female frogs probably use the spatial distribution of the nest relative to other bamboo stumps as a homing cue (Chiu and Kam, 2006). *Chirixalus eiffingeri* females appear to have good orientation abilities for nest homing, and the homing may involve some kind of route- or map-based orientation instead of direct sensory contact or trail-following, even though the mechanism remains unclear (Gould, 1986; Papi, 1992; Chiu and Kam, 2006). Additional manipulative and experimental studies need to be conducted on other anuran species that provision their tadpoles with trophic eggs to understand fully the mechanism of nest homing in these species.

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