Sex-Specific Oviposition Site Selection and Hatching Success in an Arboreal Treefrog: Implications of a Paternal Nest-Site Selection

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Abstract

Oviposition sites selected by parents is an important factor that affects offspring survival and parental fitness. A good nest site offers offspring protection from competition, predation, and harsh environmental conditions. In amphibians, though oviposition sites are generally determined by females, the distinction between male and female choice can be blurred in species with resource defense mating systems, where males occupy the territory that eggs are deposited before advertising for females. Using a phytotelm-breeding frog (*Kurixalus eiffingeri*) with male territoriality and biparental care, we examined 310 oviposition sites to determine (1) male choice based on physical characteristics of the site (stump height, inner diameter, stump depth, water depth), and (2) female choice based on site characteristics and male characteristics (snout-vent length and body condition). We hypothesized that either one or both sexes would select oviposition site based on characteristics correlate with higher offspring survivorship. We found that males preferred sites with deeper pools of water, while females showed no preference for sites or males based on the characteristics observed. While we cannot prove any nest traits directly benefit offspring, we contend that increased water depth within the phytotelm may 1) protect male frog from snake predation, which would allow for continued paternal care that increases the hatching success and 2) improve the offspring survival during the larval period. Our findings provide empirical evidence of male-driven oviposition site selection in an amphibian and highlight often overlooked role that males play in increasing their reproductive output by selecting for sites that benefit their offspring.

Significance Statement

For oviparous species, the decision of oviposition site selection affects the survival of offspring and fitness of both sexes. This study was designed to answer two questions about the oviposition site selections of arboreal Eiffingeri's frog: (1) what are the characteristics of a site affecting the oviposition site selection in both sexes, and (2) are the selected traits affect the survival of embryo? Based on results, we found the sexual differences on the oviposition site selection: males prefer a site of higher stump with deeper water inside stump, while females showed no preference. We discussed several mechanisms regarding the sexual difference in decision making. In addition, we found none of the selected site traits is related to hatching success of eggs. We contended those selected traits might relate to the survival of egg-attending male and/or tadpoles.

Introduction

Oviposition site selection, or nest site selection, is one of the key factors that determine reproductive success. A superior oviposition site can lead to increases in offspring fitness and survivorship (Howard 1978; Kolbe and Janzen 2002). Selection of oviposition sites is dependent on a number of biotic and abiotic factors, such as temperature, vegetation, predation, and presence of conspecifics (Davis 2005; Rudolf and Rödel 2005; von May et al. 2009; Pike et al. 2011; Kern et al. 2013). Though the process of selecting of a particular site can be quite complex, studies have generally focused on oviposition site selection of either males or females only (but see Howard 1978). Even though we know that animals of

different sex can respond differentially in several biological issues, such as disease resistance (Bernal and Pinto 2016), signal sensory pathway (Hoke et al. 2010), local adaptation (Svensson et al. 2018) and offspring discriminating ability (Insley et al. 2003; Ringler et al. 2016), we still have limited knowledge in the sex-specific preference of oviposition site. Similarly, while oviposition sites preference can be affected by multiple factors (Rudolf and Rödel 2005), few studies have examined the effects of and interaction between factors. A better understanding of oviposition site selection allows us to gain insight into how site suitability is determined and how characteristics that are preferred by males and females help maximize their reproductive output.

In anurans, choice of oviposition sites can depend on temperature, water volume, vegetation, competition, and predation (Howard 1978; Rudolf and Rödel 2005; von May et al. 2009). These characteristics not only affect offspring development and survival during the egg stage (Rudolf and Rödel 2005), but also have more long-lasting effects on subsequent life stages in cases where larval environment is dependent on the location of the nests. This is particularly notable in cases where larval environment is determined by nest location. In anurans, oviposition sites is often assumed to be selected or determined by females. This is because, the majority of cases, females invest more into gamete production and will often move around once amplexus is formed before settling at an oviposition site. Therefore, the significance of male preference in oviposition site selection is often overlooked. However, in resource-defense mating systems, where males occupy and defend territories (e.g. Wells 1977; Chuang et al. 2013), potential oviposition sites could be pre-selected by males before they advertise for females. The effects of male choice in oviposition site may be even more pronounced in species with higher male investment, such as those with paternal care. These factor may shift the relative weights of male and females in determining the final oviposition site. Despite the potential interplay between gamete production, resource-defense, and parental care, few studies have examined how oviposition site select differs between the sexes.

To examine the role females and males play in determining oviposition sites in a resource-defense mating system, we focused on *Kurixalus eiffingeri* (Family: Rhacophoridae), which is distributed in Taiwan and the Ryukyu islands (Kuramoto 1973; Ueda 1986). An arboreal species, *K. eiffingeri* breeds in tree holes or bamboo stumps where water has collected within the internodes (Kam et al. 1997; Kam et al. 1998a). Potential breeding sites are generally spread out within the forest. These sites are occupied by males, which defend their territories and call to attract females (Kam et al. 1996, Fig. 1). Once a female amplexus with a calling male, eggs are deposited and attached to the inner wall of the treehole or bamboo stump occupied by the male (Fig. 1). Both males and females exhibit parental care, though the timing and type of care do not overlap between the sexes. Males care for their offspring by attending the eggs (Kam et al. 1996; Chen et al. 2007; Chuang et al. 2019), while females return periodically to feed their tadpoles by laying unfertilized eggs until tadpoles reach metamorphosis (Ueda 1986; Kam et al. 1996).

Previous observations in *K. eiffingeri* indicate that only around 40% of potential breeding sites are occupied by males (Lin and Kam 2008). Since oviposition sites are not a limiting factor, males should select a given site based on the benefits it provides in increased reproductive success, via increases in

mating opportunities or offspring survivorship. Similarly, since calling males are not a limiting factor, females should select mates based on the benefits of having a preferable male or a preferable oviposition site. Given the male territoriality, female mate choice, paternal egg attendance, as well as maternal tadpole attendance, *K. eiffingeri* provides a unique case to explore factors that affect oviposition site selection between males and females. One of the main factors that affect offspring survival is egg desiccation (Lin and Kam 2008). For terrestrial-breeding amphibians, laying eggs outside of aquatic environments comes at a distinct cost, since their amniotic eggs are faced with a higher rate of evaporation in the harsh terrestrial environment. Therefore, it is not surprising that *K. eiffingeri* egg clutches are more likely to be found at oviposition sites with more water present and more potential space to accumulate water in the future (Kam et al. 1996; Lin and Kam 2008). However, what remains unknown is if males are choosing oviposition sites based on site characteristics, if females have a preference for the same site characteristics, and if the site characteristics chosen by males or females are those that correlate with offspring survivorship.

Herein, we examine how oviposition sites are selected in *K. eiffingeri* and how it affects offspring survivorship. Using natural field observations, we determine (1) if males are selecting oviposition sites based on the physical characteristics of the site (2) if females are selecting oviposition sites based on the same site characteristics and if they are selecting mates based on male characteristics. We hypothesize that males will show a preference for oviposition site characteristics that directly affect egg stage survivorship (i.e. more water and larger tree hole size). Moreover, we hypothesize that females will narrow the selection further based on the same oviposition site characteristics. Finally, we hypothesize that females will prefer larger males with better body conditions, since it may serve as an indicator of the quality of care that males are able to provide during egg attendance.

Methods

Study Site and Species

This study was conducted from July to August in 2015 & 2016 at the National Taiwan University Experimental Forest at Chitou, Taiwan (120°48'10"E, 23°39'20"N, elevation 1170 m, mean annual rainfall 2635 mm, mean annual temperature 16.6°C). We conducted observations and experiments in bamboo forests between 1900 and 0000 h. At this site, the most abundant species of bamboo are *Phyllostachys edulis* and *Sinocalamus latiflorus*, which are periodically cut for commercial purposes, leaving stumps that remain for several years before collapsing (Fig. 2). These bamboo stumps collect rain water over time and are occupied by males during the rainy season (February to August). Males will call at bamboo stumps (hereafter: oviposition sites) to attract females, which then lay eggs within the bamboo stump (Fig. 1). Once eggs hatch, tadpoles development within the breeding site until metamorphosis (Kam et al. 1996).

Experimental Design

Male choice

To examine male selection of oviposition sites, we located calling males within the bamboo forest in summer of 2015. Once males were found, we measured the following characteristics of their oviposition site: height of the bamboo stump from the ground (stump height), depth of the water within the stump internode (water depth), depth of the stump (stump depth), and the inner diameter of the stump (inner diameter). In addition, we measured the snout-vent length (SVL) and weight for each male. To compare the difference between oviposition sites that were occupied by males (male-selected sites) to those that were not (male-neglected sites), we measured site characteristics of the nearest available bamboo stump for each male-selected site. Each oviposition site was numbered and males were toe clipped for identification.

Female choice

To examine female selection of oviposition sites and female mate choice, we continued to monitor male-selected sites for presence or absence of eggs daily throughout the study period. The presence of eggs at an oviposition site was used as an indicator that they were chosen by females (female-selected sites). We then compared oviposition site characteristics and male characteristics between female-selected sites, which were male-selected sites with eggs, and female-neglected sites, which were those male-selected sites without eggs.

Egg survivorship

During the 2016 breeding season, we searched for bamboo stumps with newly-laid eggs to assess the effects of oviposition site characteristics on hatching success of eggs. We measured the site characteristics and clutch size. We then removed the attending males and covered the bamboo stump with mesh plastic mesh with 0.5 cm in diameter, which prevented attending male or other individuals from entering, but allowed for small invertebrates, such as ants, to move in and out freely. We monitored oviposition sites daily until all eggs hatched or died. We defined hatching success as nests with at least one egg successfully hatch to tadpole.

Statistical Analyses

We calculated body condition of male frog using residual of body weight and length (Baker 1992). We used Shapiro-Wilk test to assess the data normality, Wilcoxon Matched pairs test to assess the difference between male-selected and male-neglected stumps, Bonferroni method to adjust significant levels during multiple comparisons. We used Generalized Linear Mixed Model (GLMM) with binominal distribution and log as link function (i.e. logistic regression) to assess factors which affect female choice and egg hatching success: 1) female choice: we treated female-selected or neglected as dependent variables. Male body length and condition, stump height, inner diameter, stump depth, and water depth as predictive factors; 2) egg hatching success, we used egg hatching success and non-hatching success as dependent variable and stump height, inner diameter, stump depth, and water depth as predictive variable. For egg hatching success, because male frogs were removed during experiment, body characteristics were not

included in the model selection processes. We used Statistica 10 (StatSoft 2011) to perform statistical tests, and significant level is at $\alpha = 0.05$.

Results

A total of 155 paired samples (155 male-selected sites and 155 male-neglected site) were observed in this study. Stump height, stump depth, and water depth were significantly differed between male-selected and male-neglected sites (Table 1). Of the 155 male-selected sites, 27 were selected by females for oviposition (17.4%), while 128 sites remained empty throughout the observation period. Comparing female-selected and female-neglected sites, we found no significant difference in oviposition site characteristics or male characteristics (Table 2).

Table 1
Comparison of oviposition site characteristics between male-selected and male-rejected sites in *K. eiffingeri*.

Habitat traits	Used stump by male frogs (n = 155)		Non-used stump (n = 155)		Wilcoxon matched pairs test	P-value
	Median	Min-Max	Median	Min-Max		
Stump height (cm)	35.75	11.1–152	31.6	11.8–152	2.52	0.013*
Inner diameter (mm)	62	38.4-130.1	60.9	25.3–88.3	1.27	0.206
Stump depth (cm)	8.07	3.6–25.4	5.9	2-61.3	2.28	0.024*
Water depth (cm)	4.2	0.5–21.7	2.8	0.3–13.3	4.31	< 0.001*
“*” means the p-values are smaller than Bonferroni adjusted significance threshold.						

Table 2
Comparisons of oviposition site characteristics and male characteristics between female-selected (n = 128) and non-selected sites (n = 27) in *K. eiffingeri* by GLM using binominal distribution

Variables	Estimate	Standard error	Wald stat.	p-value
Intercept	0.05	3.28	0.00	0.987
Male SVL	-0.04	0.09	0.23	0.631
Male condition	0.86	0.91	0.90	0.342
Stump height	0.00	0.01	0.10	0.753
Inner diameter	0.00	0.02	0.05	0.832
Stump depth	-0.02	0.12	0.02	0.901
Water depth	0.06	0.14	0.20	0.656

We further compared the coefficient of variation (CV) of site characteristics between selected stumps and neglected stumps selected by males or females, and we found that there were no clear changes in CV in all site characteristics except the stump depth. The CV of stump depth decreased about 42 % between non-used stumps and stumps selected by males (Table 3). Results of binomial GLMM showed that none of the nest traits had significant effect on the hatching success of eggs (Table 4).

Table 3
Coefficient of variations of the physical characteristics of non-used, male-selected, and female-selected sites

CV of habitat traits (%)	Non-used stump (n = 155)	Stumps selected by males (n = 128)	Stumps selected by females (n = 27)
Stump height	59.37	63.85	66.76
Inner diameter	19.78	19.04	16.15
Stump depth	77.76	45.22	44.49
Water depth	74.39	66.92	70.83

Table 4
Logistic regression for hatching success and nest traits (n = 21).

Independent variables	Estimate	Wald statistic	Confidence interval	p-value	Stat/DF
Intercept	2.47 ± 3.20	0.59	-3.81–8.75	0.441	
Stump height	0.00 ± 0.03	0.03	-0.05–0.06	0.873	1.57
Inner diameter	-0.58 ± 0.44	1.77	-1.44–0.28	0.184	1.57
Stump depth	-0.14 ± 0.23	0.37	-0.58–0.30	0.542	1.35
Water depth	0.40 ± 0.35	1.26	-0.29–1.09	0.261	1.35

Discussion

Sex-specific oviposition site selection

The role of males in oviposition site selection in anurans has long been overlooked. The main reasons for this is two-fold, one being the relatively low male investment in gamete production, and the other being the movement of females from the calling site to the oviposition site once an amplexic pair is formed. In *K. eiffingeri*, however, males play a larger role in both determining oviposition sites and investing in post-zygotic care. Males occupy territories that are not only used to attracting females during mate selection, but also used as oviposition sites and later sites for larval development. Moreover, males provide egg attendance to increase offspring survivorship. As we predicted, males showed a significant preference for oviposition sites that held more water (Kam et al. 1996; Lin and Kam 2008). In addition, our findings indicate that oviposition site selection is primarily determined by males, with no significant differences in the sites based on female preference.

Pressure to select oviposition sites with more water may be different for males and females in *K. eiffingeri* due to the non-overlapping type and duration parental care exhibited by the sexes. Paternal care in *K. eiffingeri* is in the form of egg attendance, whereby males maintain eggs hydration by repeatedly moving between the water surface and the eggs (Ueda 1986; Chen et al. 2007; Cheng and Kam 2010). Eggs moisture is increased through water transferred by the males, which increases egg survivorship by reducing threats of desiccation and buffering eggs from harsh terrestrial environment (Shu et al. 2015). Since males are responsible for attending eggs until they hatch, water depth may affect the amount of effort males need to exert during egg attendance. In comparison, since maternal care in *K. eiffingeri* is only present during the larval stage (Ueda 1986; Kam et al. 2000; Chen et al. 2001), the discrete involving of reproduction may led females to be less sensitive to factors influencing the survival of offspring in egg stage.

Focusing on female preference more closely, characteristics between female-selected and female-neglected sites were not significantly different. However, this does not exclude the possibility of a female preference in oviposition sites. The lack of female oviposition site selection observed could be due to a

number of reasons. For instance, since oviposition sites are pre-screened by males, male-selected sites may already satisfy the criteria of females. Alternatively, variations in site characteristics may have been reduced after male selection, and therefore females may be unable to discern the difference within male-selected sites. Comparing variations in site characteristics before and after male selection (see Table 3), however, we found that the CV of most variables were similar for the potential pool of oviposition sites available for male and female choice. Assuming males and females possessed similar ability to discern differences in oviposition sites, it is unlikely that the lack of female preference is due to a lack of variation to choose from. Given the goal for both males and females is to maximize their reproductive output, we would expect the male and female preference to be driven by the same factors that affect offspring survivorship. Therefore, we suggest that females may be less selective in oviposition sites, because they are basing their preference on the same criteria for oviposition sites that had been selected for, and fulfilled by, males. A similar case of non-choosey females in a resource defense mating system with territorial males is found in strawberry poison frogs (*Oophaga pumilio*) (Meuche et al. 2013), where a minimum criteria reached by males prior to female choice is given as a potential reason for the lack of female preference.

The adaptation of oviposition site selection

Our results showed that male-selected stumps with higher stump, deeper water, and deeper stump depth, which did not significantly correlate with the hatching success of egg. However, it is possible that these factors may relate to the survival of egg-attending males and/or tadpoles in face of predation. First, an egg-attending male will either abandon its egg clutch or retreat into the water within the bamboo stump when faces a risk of predation by snakes, such as *Dinodon rufozonatum* (Colubridae) (Chuang et al. 2017). Therefore, deeper water within the stump provides a safer refuge for the egg-attending male. A higher stump and/or deeper stump depth also increases the difficulties for predators to forage. As a result, the staying of egg-attending males would increase the egg survivorship (Chuang et al. 2019). Secondly, the selection of deeper water by males may relate to the tadpole survival. Desiccation is a major source of larval mortality in ephemeral habitats (Newman 1988; Gomez-Mestre et al. 2013), and it is especially true for phytotelmic habitats which are only able to hold a small volume of water (Lehtinen 2004; Rudolf and Rödel 2005). We contend that deeper water within bamboo stumps is therefore critical to the growth and survival of tadpoles. Larval period in *K. eiffingeri* ranges from 40–78 days (Kam et al. 1998b), and the water levels are known to fluctuates temporally (Lin and Kam 2008). Therefore, stumps with deeper water are able to provide water persistence, and tadpoles are less prone to suffer mortality due to habitat desiccation. Furthermore, tadpoles that live in stumps with deeper water are potentially facing lower risk of snake predation because they are able to retreat to the lower part of water body to seek a refuge. Hu (2017) described the foraging behavior of *L. ruhstrati ruhstrati*, a predator of *K. eiffingeri* tadpoles, as submerging anterior part of its body in the water and swinging its anterior laterally, forming a fan-shaped area. As soon as the snake's snout touched a tadpole, the snake opened its mouth, bit the tadpoles, and resurfaced to consume it. Hu (2017) postulated that smaller stump and deeper water within the stumps make it difficult for the snake to maneuver in the water to prey on tadpoles while maintaining body balance, and deeper water could provide more space for tadpoles to escape.

Conclusion

In conclusion, our study compares oviposition site selection in males and females in an amphibian species with male territoriality. We examine how differences in reproductive strategy and parental investment between the sexes can influence the decisions made when picking an oviposition site. Results indicate that oviposition site selection in *K. eiffingeri* is driven by males and occurs prior to female-driven mate choice. However, site characteristics do not correlate with hatching success of egg, but might relate to the survival of egg-attending male and/or tadpoles. Future studies examining the relationship between male-selected site characteristics and egg, tadpole, and attending male survivorships directly are needed to elucidate the factors driving male preference. Overall, our findings highlight the important, but often overlooked, role male play in determining oviposition sites. With increased male investment, whether in territorial defense or parental care, we may find that male preference in oviposition site selection is more pronounced than previously known.

Declarations

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Compliance with ethical standards

Ethical approval: All research presented in this manuscript was conducted in accordance with ethical standards of Tunghai University and was approved by the Institutional Animal Care and Use Committee of Tunghai University (No. 100-19). Experiments at Chitou were approved by the College of Bio-Resources and Agriculture, National Taiwan University (Document No. 1030006132). No other permits were required because these field studies were not conducted in a protected area nor were our subjects an endangered or protected species.

Conflict of interest: The authors declare that they have no conflict of interest.

Data availability: All data generated and analyzed during this study are included in the supplementary information file of this published article (Supplementary File 1).

Authors contribution

MFC and YCK conceived of the study; MFC and NTF collected the data; MFC and SP analysed the data; MFC, SP and YCK wrote the initial manuscript; all authors edited and approved the final manuscript.

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Figures

Figure 1

Left: *Kurixalus eiffingeri* male occupying water-filled bamboo stump and advertising for females. Right: *K. eiffingeri* male attending eggs after successful mating event. Bamboo stumps are used as oviposition sites where eggs, and later tadpoles, develop.

Figure 2

Bamboo forest at Chitou, Taiwan. Stumps from fallen, or cut, bamboo are used as calling and breeding sites by *Kurixalus eiffingeri*.

Supplementary Files

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