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Sex-specific oviposition site selection in an arboreal treefrog with a resource-defense mating system

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Abstract

Oviposition site selection by parents is an important factor that affects offspring survival and parental fitness. The relative importance of sexes in oviposition site selection in anurans is rarely evaluated, especially in species with resource-defense mating systems, where males defend territory containing eventual oviposition sites before advertising for females. Using a phytotelm-breeding frog (*Kurixalus eiffingeri*) with male territoriality, we examined 310 bamboo stumps (potential for oviposition sites) to determine whether male and female choice of oviposition site based on physical characteristics (stump height, inner diameter, stump depth, water depth, and water volume). We found that males preferred a site with higher stumps that were deeper and contained more water, while females showed no preference for sites based on the characteristics observed. Although we do not exclude the possibility that *K. eiffingeri* female oviposition site selection can be relied on and/or correlates to male advertisement calls, this study is one of few studies to examine the role of both sexes in oviposition site selection simultaneously, and provides empirical evidence that oviposition site selection is primarily determined by males in an amphibian with a resource-defense mating system.

KEYWORDS

nest-site selection, phytotelm-breeding, resource-defense mating system, sexual difference, territoriality

1 | 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 & Janzen, 2002). The selection of oviposition sites is dependent on a number of biotic and abiotic factors, such as temperature, vegetation, predation, and the presence of conspecifics (Davis, 2005; Kern et al., 2013; Pike et al., 2011; Rudolf & Rödel, 2005; von May et al., 2009). While the process of selecting a particular site can be quite complex, studies have generally focused on oviposition site selection by either males or females only (but see Howard, 1978). Even though we know that responses can differ between the sexes in a number of aspects, including disease resistance (Bernal & 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 have limited knowledge in the sex-specific preference of oviposition site.

Anurans exhibit a wide range of mating systems, from lek-chorusing mating systems to resource-defense mating systems

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(Wells, 1977a, 2007), which can vary in the relative importance of that male and female choice when it comes to oviposition site selection. In lek-chorusing species, males aggregate to form choruses and call to attract females. Females enter the choruses to choose their mates. When the mating pairs are formed, females carry males and move to an oviposition site (e.g., Cheng et al., 2022). Therefore, females appear to play a more important role in oviposition site selection in lek-breeding species (Halloy & Fiaño, 2000; Kiesecker & Skelly, 2000). On the contrary, in resource-defense species, males first defend territories that function as oviposition sites and then call to attract females. (e.g., Chuang et al., 2017; Wells, 1977b). In such circumstances, oviposition sites are selected by males before they advertise for females (Mitchell, 2001, 2002), and therefore, males are assumed to play a more important role than females in oviposition site selection. However, this assumption is rarely tested and few studies have evaluated the roles of males and females in oviposition site selection within the same species to confirm their relative importance.

In anurans, the choice of oviposition sites can depend on temperature, water volume, water chemistry, vegetation, competition, and predation (Fouilloux et al., 2021; Howard, 1978; Rudolf & Rödel, 2005; Touchon & Worley, 2015; von May et al., 2009). These characteristics not only affect offspring development and survival during the egg stage (Rudolf & Rödel, 2005) but also have more long-lasting effects on subsequent life stages in cases where the larval environment is dependent on the location of the nests. One unique type of oviposition sites utilized by anurans are phytotelms, which are small pools of water that accumulate within parts of a plant (e.g., tree holes, bamboo stumps, leaf axils, etc.) (Fischer, 2023; Srivastava et al., 2004). These water bodies are lentic and usually ephemeral, characterized by their small size and discreteness. Therefore, phytotelm-breeding species provides the opportunity to measure the physical characteristics of individual oviposition sites easily and accurately (Lehtinen et al., 2004; Poelman et al., 2013).

To examine the role males and females play in determining oviposition sites in a resource-defense mating system, we used *Kurixalus eiffingeri* (Family: Rhacophoridae), which is distributed in Taiwan and the Ryukyu islands (Kuramoto, 1973; Ueda, 1986). As a phytotelm-breeding species, *K. eiffingeri* breeds in tree holes or bamboo stumps where water has collected within the internodes (Kam et al., 1997; Kam, Hsu, et al., 1998). Potential breeding sites are generally spread out within the forest. These sites are occupied by males, which acoustically and physically defend their territories and call to attract females (Chen et al., 2011; Kam et al., 1996). Once a female form amplexus with a calling male, eggs are deposited at the site occupied by the male (Figure 1). Eggs are attached to the inner wall of the treehole or bamboo stump, above the water surface, with tadpoles dropping into the small pool once they hatch. Both males and females exhibit parental care in this species. Males care for their offspring by attending the eggs (Chen et al., 2007; Chuang et al., 2019; Kam et al., 1996), while females return periodically to feed their tadpoles by laying unfertilized eggs until tadpoles reach metamorphosis (Kam et al., 1996; Ueda, 1986). As other phytotelmata, the water levels of bamboo stump can fluctuate greatly depending upon the balance between evaporation and rainfall (Caldwell & de Oliveira, 1999; Lin & Kam, 2008; Wassersug et al., 1981). The water volume within bamboo stumps can increase rapidly on rainy days (Lin & Kam, 2008). Similarly, the water temperature within these small pools can change rapidly and fluctuate with air temperature (Kam et al., 2001). The combination of a resource-defense mating system and the phytotelm-breeding nature of *K. eiffingeri*, this species provides an opportunity to explore factors that affect oviposition site selection between males and females. In this study, our aim is to determine whether males and females are selecting oviposition sites based on the physical characteristics of the site. As a species with a resource-defense mating system, we hypothesize that males play an important role in oviposition site selection. However, because oviposition site characteristics, especially water volume, can fluctuate over time, we also hypothesize that females will play a role in oviposition site selection in addition to selecting suitable males.

2 | METHODS

2.1 | Study site and species

This study was conducted from July to August in 2015 and 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 between 07:00 p.m. and 12:00 a.m. in bamboo forests with a total surface area of roughly 2.5 hectares. 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

FIGURE 1 Left: *Kurixalus eiffingeri* male occupying a 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.

before collapsing (Figure 1). These bamboo stumps collect rainwater 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 (Figure 2). Once eggs hatch, tadpoles develop within the phytotelm until metamorphosis (Kam et al., 1996).

2.2 | Experimental design

2.2.1 | Male choice

To examine male selection of oviposition sites, we located calling males within the bamboo forest from July 13, 2015 to August 18, 2015. A total of 155 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). We calculated the water volume of the stumps (water volume) using $\pi r^2 h$ (r: inner radius of stumps, h: water depth). In addition, we measured the snout-vent length (SVL) by caliper (to the nearest .01 cm) and weight by a portable electric scale (to the nearest .1 g) for each male. We calculated the body condition of males using the scaled mass index (SMI) (Peig & Green, 2009), which was calculated from the body length and body weight according to the following equation: $SMI = Mi[L_0/Li]bSMA$, where Mi and Li were the body weight and the SVL of individual i, respectively; bSMA was the scaling exponent estimated by the standardized major axis (SMA) regression of ln body weight on ln SVL; and L_0 was the mean body length of study population. 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 with water for each male-selected site. The distance for each male-selected site and male-neglected site is provided in Supplementary Materials (Supplementary File 1 data), the average distance is 171.5 cm, ranging from 10.6 to 957 cm. Each oviposition site was numbered, and males were toe-clipped for identification.

FIGURE 2 Bamboo forest at Chitou, Taiwan. Stumps from fallen or cut bamboo are used as calling and breeding sites by *Kurixalus eiffingeri*.

2.2.2 | Female choice

To examine female selection of oviposition sites, we continued to monitor male-selected sites for the presence or absence of eggs daily throughout the study period. The presence of eggs at 27 oviposition sites 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. We surveyed bamboo stumps in the study area daily, thus the possibility that stumps observed without eggs were a result of eggs being consumed by predators before the surveyors arrived is very low.

2.3 | Statistical analyses

We used the Shapiro–Wilk test to assess the data normality and the Wilcoxon matched pairs test to assess the difference between male-selected and male-neglected sites. We used Spearman correlation coefficients (r_s) to examine the significance of the correlations between male characteristics and site characteristics. To reduce the number of dimensions and avoid multicollinearity, we used a principal component analysis (PCA) with varimax rotation to condense the five site characteristics and two male site characteristics. We then used the generalized linear model (GLM) with binomial distribution and log as link function (i.e., logistic regression) to assess these principal components (PCs) that affect female choice. We used PCs as predictive variables and female site selection (selected or neglected) as dependent variables. We used Statistica 10 (StatSoft, 2011) to perform statistical tests, and the significant level was set at $\alpha = .05$.

2.4 | Ethics note and STRANGE statement

All research presented in this manuscript was conducted in accordance with the 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 and our study species was not an endangered or protected species.

The STRANGE framework (Webster & Rutz, 2020) serves to enhance transparency by identifying potential sampling biases in animal behavior research. This framework encompasses factors such as social background, trappability and self-selection, rearing history, acclimation and habituation, natural changes in responsiveness, genetic makeup, and experience. We believe that there is a low level of bias, if any, in our research based on the STRANGE framework because we conducted this study in the field. However, there remains a potential for sampling bias in our study due to the following reasons: (1) frogs were sampled within a single population, (2) only a subset of the population, that is, those observed in the bamboo stumps during breeding season, was studied, and (3) the age of the frogs was not determined.

3 | RESULTS

A total of 155 paired samples (155 male-selected sites and 155 male-neglected sites) were observed in this study. We found that males preferred sites with higher stumps that were deeper and contained more water (Table 1; Figure 3). For the males who used stumps, we found that male body length (SVL) was positively and significantly correlated with stump depth and male body condition was positively and significantly correlated with stump depth, water depth, and water volume (Table 2; Figure 4). In other words, males that were

TABLE 1 Comparison of oviposition site characteristics between male-selected and male-neglected sites in *Kurixalus eiffingeri*.

	Male-selected sits ($n = 155$)		Male-neglected sites ($n = 155$)		Wilcoxon-matched pairs test	
Characteristics	Median	Min-max	Median	Min-max	W-value	*p*-value
Stump height (cm)	35.8	11.1–152.0	31.6	11.8–152.0	1280.5	.022*
Inner diameter (mm)	62.0	38.4–130.1	60.9	25.3–88.3	627.0	.264
Stump depth (cm)	8.1	3.6–25.4	5.9	2.0–20.1	2509.5	<.001*
Water depth (cm)	4.2	.5–21.7	2.8	.3–13.3	2562.0	<.001*
Water volume (mL)	124.6	10.4–1394.1	7.5	4.3–814.0	2221.0	<.001*

Note: * represents the oviposition site characteristics are significantly different between groups.

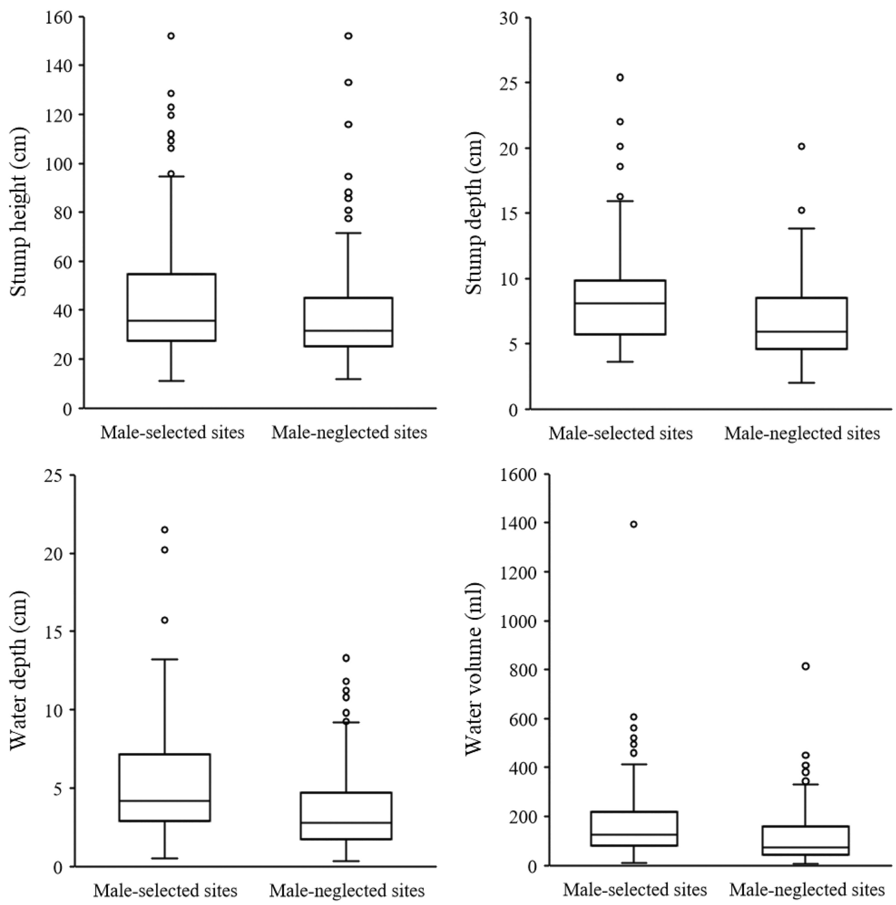

FIGURE 3 Oviposition site characteristics, including: stump height, stump depth, water depth, and water volume, at sites that were selected by males ("male-selected sites") and not selected by males ("male-neglected sites"). The line inside the box represents the median, and the bottom and top of the box refer to the first and third quartiles. Open circles represent outliers.

larger and in better condition used the stumps with deeper depth, and males with better condition used the stumps containing more water (Table 2; Figure 4).

Of the 155 male-selected sites, 27 were selected by females for oviposition (17.4%), while 128 sites remained empty throughout the observation period. Using principal component analysis (PCA) with varimax rotation, we constructed four composite variables (PCs) that together explained 89.8% of total variance. The first PC (PC1) reflects the stump height, stump depth, water depth, and water volume, the second PC(PC2) reflects inner diameter and water volume, PC3 reflects male SVL, and PC4 reflects male condition (Table 2). Comparing female-selected and female-neglected sites, we found no significant difference in oviposition site characteristics or male characteristics (Table 3).

4 | DISCUSSION

As predicted, males showed a significant preference for oviposition sites that held more water. For terrestrial-breeding amphibians, laying eggs outside aquatic environments comes at a distinct cost, because their amniotic eggs are faced with a higher evaporation rate in terrestrial environments. High evaporation rates can lead to dehydration and egg stage mortality (Chuang et al., 2019; Kam, Hsu, et al., 1998). Since potential oviposition sites are not a limiting factor (Lin & Kam, 2008), it is logical that males would show a preference for sites that contain more water and give their offspring a better chance at survival. Previous studies have also shown that *K. eiffingeri* egg clutches are more likely to be found at oviposition sites with more water present and more potential space to accumulate

TABLE 2 Spearman correlations between male characteristics and site characteristics in *Kurixalus eiffingeri*.

Male characteristics	Stump height (cm)	Inner diameter (mm)	Stump depth (cm)	Water depth (cm)	Water volume (mL)
Male SVL (mm)	.03 (.698)	−.04 (.580)	.22 (<.05*)	.11 (.161)	.10 (.194)
Male body condition	.00 (.927)	.15 (.07)	.20 (<.05*)	.17 (<.05*)	.20 (<.05*)

Note: The Spearman's correlation coefficient (r_s) are reported on the upper rows. *p*-values are reported in parentheses. * represents the significant relationship between two traits.

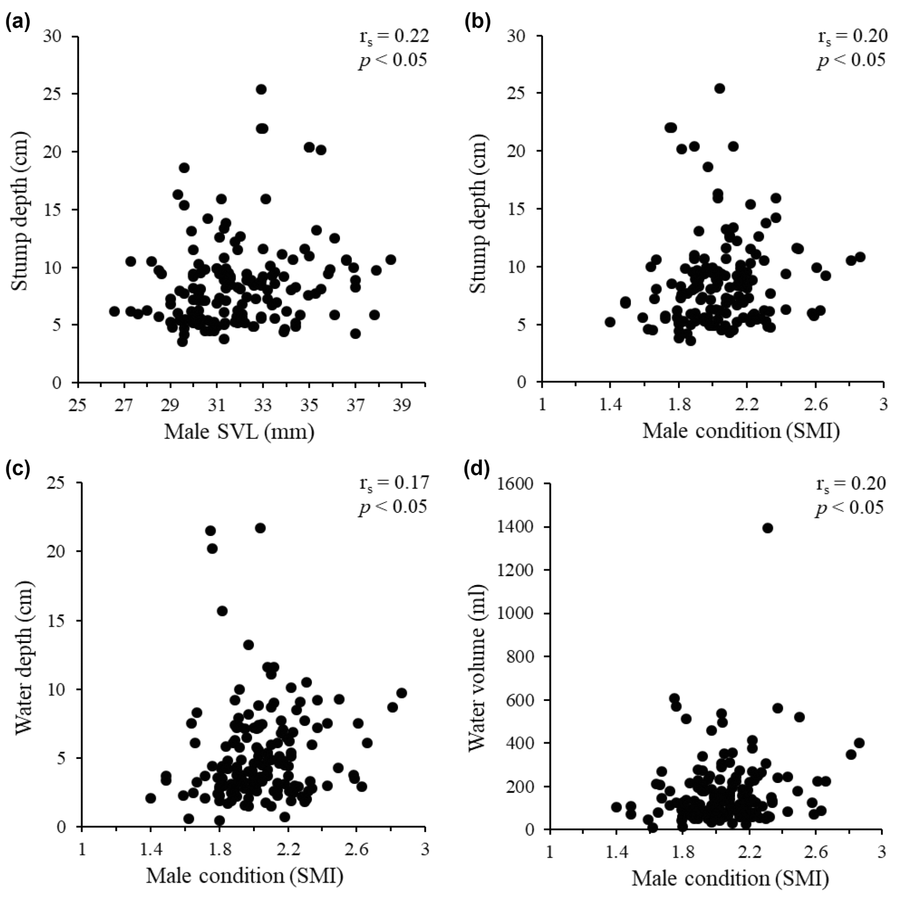

FIGURE 4 Significant relationships between (a) male body size (SVL) and stump depth, and between male condition (SMI) and (b) stump depth (c) water depth, and (d) water volume, respectively.

water in the future (Kam et al., 1996; Kam, Hsu, et al., 1998; Lin & Kam, 2008). In *K. eiffingeri*, males maintain egg hydration by repeatedly moving between the water surface and the eggs (Chen et al., 2007; Cheng & Kam, 2010; Ueda, 1986). Egg moisture is maintained through water transferred from the males, which is critical for egg survival (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. Moreover, deeper water within stumps may increase tadpole survival. Desiccation is a major source of larval mortality in ephemeral habitats (Gomez-Mestre et al., 2013; Newman, 1988), and it is especially true for phytotelmic habitats, which are only able to hold a small volume of water (Lehtinen, 2004; Rudolf & Rödel, 2005). The larval period in *K. eiffingeri* ranges from 40 to 78 days (Kam, Lin, et al., 1998). Therefore, deeper water within bamboo stumps is critical to the growth and survival of tadpoles. Furthermore, tadpoles that live in stumps with deeper water are potentially able to retreat into the depth of the water to avoid predation from snakes, such as *Lycodon ruhstrati ruhstrati* (Hu, 2017). These considerations combined, a higher stump with a deeper pool of water presents a number of advantages to offspring survival, making it a good quality oviposition site that is preferred by males.

Focusing on female preference, site characteristics between female-selected and female-neglected sites were not significantly different, suggesting females do not choose oviposition sites based on site characteristics. The results were inconsistent with the previous studies in anurans (e.g., O'Brien et al., 2020; Rudolf & Rödel, 2005). In *Pseudophryne coriacea*, a terrestrial-breeding frog, males construct small chambers (nests) among soil, leaf litter, or woody debris, while females choose oviposition sites based on nest moisture (O'Brien et al., 2020). In *Phrynobatrachus guineensis*, a phytotelm-breeding species, females select oviposition sites based on the frequency that water was present at the site (Rudolf & Rödel, 2005). The discrepancies between our results and those from previous studies may be due to different analytic methods. In the studies in *Pseudophryne coriacea* and *Phrynobatrachus guineensis*, the authors examined the difference in site characteristics between "egg-presence" and "egg-absence" sites (O'Brien et al., 2020; Rudolf & Rödel, 2005). Using this type of quantification meant that "egg-absence sites" included both sites that were "selected by males and neglected by females" and "neglected by both males and females." However, in our study, we examined female preference on the site characteristics after male selection. Therefore, we compared the different characteristics between sites that were "selected by males and females" (i.e., "egg-presence") and sites that were "selected by males but neglected by females." Given the reproductive behavior of *K. eiffingeri*, the analytic method we employed is more reasonable to examine the role of sexes in oviposition sites in this species (Table 4).

Our results also showed that females had no preference for male size (SVL) and body condition. A similar case of non-choosey females is found in strawberry poison frogs (*Oophaga pumilio*) (Meuche et al., 2013). Interestingly, in our study, male traits were correlated with bamboo stump quality. Therefore, the lack of female choice suggests that females are not using male SVL and condition as indicators for mate choice. Moreover, females not using oviposition site characteristics are a signal for nest site selection. However, we do not exclude the possibility that *K. eiffingeri* female mate choice is based on other factors such as male advertisement calls (Cui et al., 2011; O'Brien et al., 2020), since most anurans use acoustic signals to convey information during social and reproductive interactions (Gerhardt & Huber, 2003; Wells & Schwartz, 2007).

In conclusion, our study indicates that oviposition site selection in *K. eiffingeri*, a species with a resource-defense mating system, is primarily determined by males. Although there may be additional factors influencing female selection that are not measured in the current study, we highlight the importance of considering the role

TABLE 3 Loadings of the four principal components of oviposition site characteristics and male characteristics in *Kurixalus eiffingeri*.

	Principal components			
Characteristics	PC1	PC2	PC3	PC4
Stump height (cm)	**.779**	−.307	−.159	.020
Inner diameter (mm)	−.019	**.941**	−.066	.072
Stump depth (cm)	**.884**	.220	.197	.054
Water depth (cm)	**.927**	.169	.100	.034
Water volume (mL)	**.660**	**.694**	.031	.091
Male SVL (mm)	.079	−.053	**.967**	−.156
Male body condition	.065	.088	−.155	**.982**
Eigenvalues	2.70	1.55	1.04	1.01
% of variance	38.49	22.13	14.84	14.37

Note: The cumulative variance of the first four principal components is 89.83%. Bold value indicates loadings greater than .6.

TABLE 4 Comparisons of oviposition site characteristics and male characteristics between female-selected and female-neglected sites in *Kurixalus eiffingeri* by GLM using binomial distribution.

	Female-selected sites (*n* = 27)		Female-neglected sites (*n* = 128)		GLM (binomial distribution)			
Variables	Mean	*SE*	Mean	*SE*	Esti	*SE*	Wald stat.	*p*-value
PC1	.07	.20	−.02	.09	.09	.21	53.7	.677
PC2	.01	.17	−.00	.09	.01	.21	.2	.949
PC3	−.04	.16	.01	.09	−.04	.21	.0	.838
PC4	.17	.20	−.04	.09	.21	.21	1.0	.322

of both sexes simultaneously when examining oviposition site selection. In addition to our study, oviposition site selection has been studied in various animal taxa (e.g., insects, fish, amphibians, reptiles, and birds) (Refsnider & Janzen, 2010). In birds with territorial behavior, a number of studies have emphasized or focused on the role of one sex (i.e., male) (Fernández & Reboreda, 2002; Jones & Robertson, 2001), though there are some that suggest females play an important role in the process of determining nest sites (Alatalo et al., 1986; Chiaradia et al., 2019). By examining the relative roles of males and females in more detail, our findings, along with that of previous studies, contribute to a broader understanding of the ecological and evolutionary significance of nest site selection across taxa.

AUTHOR CONTRIBUTIONS

Sinlan Poo: Conceptualization; formal analysis; writing – original draft; writing – review and editing; validation. **Yuan-Cheng Cheng:** Data curation; conceptualization; writing – review and editing; project administration; visualization; software. **Nien-Tse Fuh:** Methodology; investigation; formal analysis; data curation; validation. **Ming-Feng Chuang:** Writing – original draft; visualization; investigation; supervision; project administration; methodology; writing – review and editing; validation. **Yeong-Choy Kam:** Conceptualization; funding acquisition; project administration; supervision; resources; writing – review and editing; software; validation.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

All data generated and analyzed during this study are included in the Supplementary Information file of this published article (Supplementary File 1).

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