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Selection of calling sites by *Pelophylax porosus porosus* (Anura: Ranidae)

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Abstract In frogs, males generally use calls to attract conspecific females for breeding. Previous studies suggest that male frogs can effectively attract females by calling from an open environment, which has the advantages of avoiding the diminishing of their calls and increasing attractiveness to females by bimodal (acoustic + visual) signal. However, males calling from open sites, would be more easily detected by predators due to their exposed bodies. Male frogs may need to select a calling site that is suitable for environmental conditions to enhance their survival rate and mating success. In the present study, we examined the selection of calling sites by *Pelophylax porosus porosus* male, whose predators are mostly diurnal. As a results, *P. p. porosus* males tended to select vegetation-shaded water surfaces as daytime calling sites and select open water surfaces as night calling sites. Our results suggest that choice of calling sites by *P. p. porosus* males depends on whether it is daytime or night, because of differences in predation risk between daytime and night. The selection of a calling site suitable for each situation is expected to increase the fitness of the male frogs.

Wybór miejsc nawoływania przez *Pelophylax porosus porosus* (Anura: Ranidae)

Słowa kluczowe żaba, płazy, zachowania godowe, zagrożenie drapieżnicze

Streszczenie U żab, aby się rozmnożyć samce zazwyczaj nawołują, aby zwabić samice swojego gatunku. Wcześniejsze badania sugerują, że samce żaby mogą skutecznie wabić samice, wołając z otwartego środowiska, co ma tę zaletę, że pozwala uniknąć tłumienia ich nawoływań (np. przez roślinność) i zwiększania atrakcyjności dla samic za pomocą sygnału bimodalnego (akustycznego + wizualnego). Jednak samce nawołujące z otwartych miejsc byłyby łatwiej wykrywane przez drapieżniki (brak możliwości ukrycia się). Samce żab mogą wybierać miejsca wołania, optymalizując swoją przeżywalność i sukces lęgowy. W niniejszej pracy zbadano dobór stanowisk nawoływania przez samca *Pelophylax porosus porosus*, który jest zagrożony drapieżnictwem w ciągu dnia. W rezultacie samce tego gatunku miały tendencję do wybierania zacienionych przez roślinność powierzchni wody jako miejsc do przebywania w ciągu dnia i wybierały powierzchnie wód otwartych jako miejsca do nawoływań nocnych. Nasze wyniki sugerują, że wybór miejsc nawoływania zależy od tego, czy jest dzień, czy noc, ze względu na różnice w ryzyku drapieżnictwa między dniem a nocą. Wybór odpowiedniego miejsca nawoływania zwiększa liczbę wyprowadzonego potomstwa jednocześnie minimaluzując prawdopodobieństwo śmierci w wyniku drapieżnictwa.

Introduction

In anuran amphibians (frogs), males generally use acoustic signals (calls) to attract conspecific females for breeding (Wells, 1977; Arak, 1983; Ryan, Keddy-Hector, 1992). Vocal characteristics, such as frequency, intensity, complexity, and calling rate are important in increasing attractiveness to females (Ryan, Keddy-Hector, 1992; Grafe, 1997; Taylor, Buchanan, Doherty, 2007), but environmental characteristics of calling sites are also important (Fellers, 1979). For example, in *Hyla versicolor*, males that are successful in attracting females tend to select perches which are horizontal and had relatively less vegetation in the immediate vicinity as calling sites (Fellers, 1979). Fellers, (1979) reported that a perch with little surrounding vegetation is less likely to diminish the call by vegetation, and that the horizontal nature of the perch allows for a uniform spreading of the call, and described the advantages of an open calling site. In *Physalaemus pustulosus*, females prefer an acoustic signal combination including vocal sac inflation (bimodal signal: acoustic + visual signals) over an identical set of signals with the vocal sac inflation removed (unimodal signal) (Rosenthal, Rand, Ryan, 2004; Taylor, Klein, Stein, Ryan, 2008). A similar increase in calling male attractiveness by bimodal signal combined acoustic and visual signals has also been observed in some hylid frogs, such as *H. squirella*, *H. arborea* (Taylor et al., 2007; Gomez et al., 2009). Under natural field conditions, only a few of the males in a chorus are likely to be visible to females if there vegetation cover and heterogeneity of the substrate (Taylor et al., 2007, 2008). In those cases, males that are visually accessible to the females may increase their probability of being selected as mates (Taylor et al., 2007, 2008). The results of these previous studies suggest that male frogs can effectively attract females by selecting an open environment as a calling site, which has the advantages of avoiding the diminishing of their calls and increasing attractiveness to females by bimodal signal. However, males calling from open sites, which are considered advantageous in attracting females, would be more easily detected by predators due to their exposed bodies. Furthermore, conspicuous breeding behaviors, such as vocalizations by male frogs, increase predation risk (Magnhagen, 1991). To attract females for breeding under high predation risk, males may need to use risk mitigation behaviors such as calling while hiding. It is necessary to explore the balance between attractiveness to females and predation risk factors in calling site selection by males to understand the evolution of breeding behaviors and strategies in frogs. However, the relationship between calling site selection and predation risk of males, and attractiveness to females in frogs is still unknown.

Pelophylax porosus porosus is a medium-sized frog that is endemic to Japan and naturally distributed only in Honshu main island (Matsui, Maeda, 2018). This frog inhabits still waters such as paddy fields and ponds. It breeds in these still water environments from late April to July (Matsui, Maeda, 2018). During the breeding season, the male calls while floating on the water surface, with his vocal sacs on both cheeks inflated greatly to attract conspecific females (Shimoyama, 1989; Matsu, Maeda, 2018). After mating, breeding pairs move outside the calling sites to search for ovipositional sites, distributing eggs from a single clutch over several sites

(Shimoyama, 1989; Matsui, Maeda, 2018). Thus, in *P. p. porosus*, male calling sites function only as sites to attract females (Shimoyama, 1989).

The paddy fields and ponds inhabited by *P. p. porosus* are also the habitats of birds such as herons, gray-faced buzzards, and snakes, which are its major predators (Kosugi, 1960; Fukada, 1964; Yamada, 1994; Kadowaki, 1996; Takumi, Ezaki 1998; Momose et al., 2005; Edirisinghe, Bambaradeniya, 2006; Sakai, Yamaguchi, Momose, Higuchi, 2011). These predators are diurnal (Kosugi, 1960; Fukada, 1964; Kadowaki, 1992, 1996; Yamada, 1994; Momose et al., 2005; Sakai et al., 2011), meaning that *P. p. porosus* is exposed to high predation risk during the daytime.

We hypothesized that *P. p. porosus* males select hidden calling sites during daytime when predation risk is high but select open sites favorable for attracting females at night. In the present study, we aimed to examine this hypothesis by observing the calling sites of *P. p. porosus* in a semi-natural field, where several ponds with different environmental conditions were created. Based on observational data, we discuss the relationship between decision of calling sites and attractiveness to females, as well as the predation risk at calling sites.

Materials and Methods

Frogs

Pelophylax porosus porosus were collected from paddy fields in Fujisawa City, Kanagawa Prefecture, Japan. Sexually mature males were used for the experiments. The sex was determined based on the presence or absence of secondary sexual characteristics, such as nuptial pads and external vocal sacs (Matsui, Maeda 2018). Snakes and herons inhabit the paddy fields where the experimental specimens were collected, and we actually encountered *Rhabdophis tigrinus* and *Egretta garzetta* preying on *P. p. porosus* males several times in the daytime.

Experimental field

The experimental field of the present study is shown in Figure 1.

We conducted the experiment in a net room (bottom: 2.5 × 4.8 m, height: 2 m). The net room was created by wrapping insect-repelling nets around the framework of a horticultural vinyl greenhouse. Four ponds measuring 1.53 m^2 (0.85 × 1.8 m) each were created by embedding a blue waterproof sheet on the ground inside the net room. Two ponds were 30 cm deep and the other two were 10 cm deep, but the water surface area of all four ponds were identical. Vegetation was planted on the banks of the northern half of the net room, and the southern half remained vegetation-free. The vegetation comprised the species that occur naturally on the banks of paddy fields from which *P. p. porosus* were collected, such as *Setaria viridis*, *Eleusine indica*, *Rumex acetosa*, and *Plantago asiatica*.

During the experiment, the planted vegetation was pruned and maintained at a height of approximately 30 cm. The two ponds that were surrounded by banks with vegetation were called the “vegetated ponds,” and the other two ponds that were surrounded by banks without vegetation were called the “non-vegetated ponds.” In the vegetated ponds, vegetation on the bank covered the water surface within 10 cm from the edge, creating shaded conditions. In contrast, no vegetation covered the water surface farther than 10 cm from the shoreline, creating an open water surface. In the non-vegetated ponds, there was no vegetation cover, and water surface was uniformly open. We pasted numbered vinyl tapes at 10 cm intervals along the banks to record the sites from

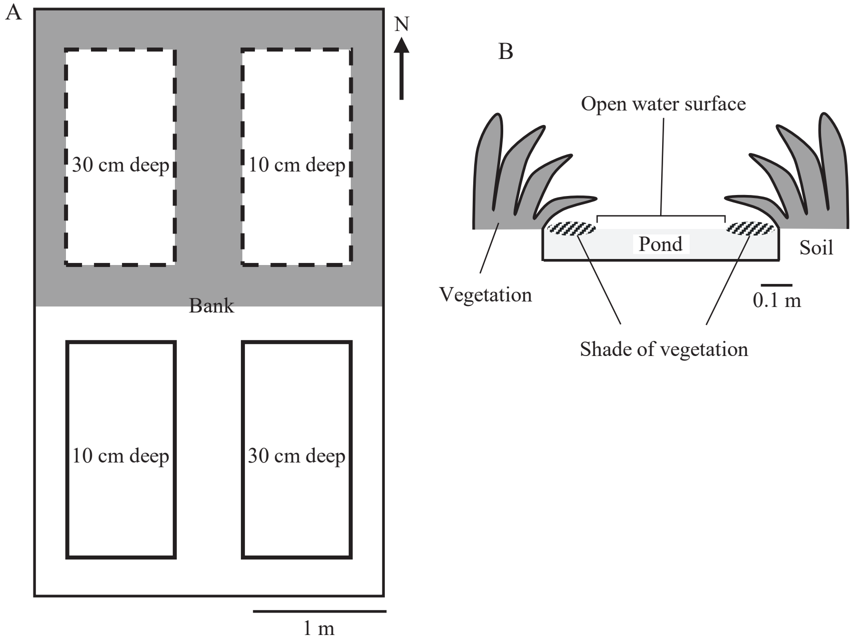

Figure 1. The layout of experimental field. A. The view from above. The gray zone is planted with vegetation. The dotted rectangles represent the vegetated ponds, and the solid rectangles represent the non-vegetated ponds, respectively. B. The cross-sectional view of a 10-cm deep vegetated pond

which male frogs were calling. The sites were recorded to the nearest 5 cm. The upper part of the experimental field was not covered by trees, and the light environment was the same in all the four ponds. In addition, there was no artificial light source in the vicinity of the experimental field.

Experimental methods

Experiments were conducted from May 14 to June 28, 2018, and from May 5 to June 20, 2019. These periods fell within the breeding season of the *P. p. porosus* population that was used in the experiments. In both years, trials of 7 days were set several times using the same 12 individual frogs that were replaced in each trial. From the preliminary surveys, we established that a maximum of three *P. p. porosus* males call from the puddle water surface of about 1.5 m^2. In the present study, four ponds measuring about 1.5 m^2 were used, and the number of experimental individuals per trial was set to 12, assuming that three males would call from each pond if there is no tendency to select a particular pond as a calling site. In 2018 and 2019, four and three trials were conducted, respectively. Therefore, a total of 84 male *P. p. porosus* were used in our experiment. Frogs were collected at night and released into the center of the net room immediately after collection, and observations were made from mid-day (12:00) of the next day. We did not feed the experimental frogs because there were many insects and spiders in the net room for the frogs to prey on. After each trial, the frogs were released into the paddy field from which they were collected, and the pattern of their dorsal surface was recorded to prevent duplication of use between trials. Colored threads were wrapped around the waists of the frogs to identify individuals. Observations were made twice through the day, during the daytime (12:00) and at night (0:00), and each observation period was approximately 20 min. Observations were done with the naked eye, and the net room was illuminated with lights (LH-PY01Z-S, OHM ELECTRIC Inc, Tokyo, Japan) at night. There was no apparent disruption of the frog's behavior by the illumination of the lights. We defined a calling male as a male emitting an advertisement call. The sites of calling males (calling sites) were recorded during each observation. If the calling males moved during a single observation, they were recorded at the first site where they were observed.

Data analysis

Out of a total of 84 frogs used in the experiment, 69 males emitted an advertisement call during the experiment, and a total of 370 calling site data were obtained from these 69 males. In the following analysis, we used the 370 calling site data obtained from the experiment.

We hypothesized that vegetated ponds, which have shelters (shade of vegetation), are selected as calling sites during daytime when predation risk is high whereas non-vegetated ponds, which are open and more favorable for attracting females, are selected at night. In paddy fields and ponds, which are the breeding habitat of *P. p. porosus*, variations in water depth are common. These differences in water depth lead to differences in environmental factors such as water temperature, which may in turn influence the selection of calling sites. It is possible that the frogs acclimatized to the experimental field with the passage of days since the start of the experiment, because the same frogs were used for 7 days of observation. Thus, the number of days since the frogs were released into the net room may also affect the determination of the calling site (same for the next analysis). Therefore, we conducted a generalized linear model (GLM) analysis with the pond type selected as the calling site (vegetated pond = 1, non-vegetated pond = 0) as the response variable, observation time (daytime = 1, night = 0), water depth (30 cm = 1, 10 cm = 0), and number of observation days (1–7) as explanatory variables, the binomial distribution as the error distribution, and the logit link function as the link function.

In the vegetated ponds, the water surface within 10 cm from the edge was shaded by vegetation (Figure 1), where males can call while hiding. The distribution of calling sites on the water surface of the vegetated ponds is predicted to be concentrated within 10 cm from the edge (shade of vegetation) during the daytime, when predation risk is high but this tendency is not expected at night during which predation risk is low. In contrast, there was no vegetation cover in the non-vegetated ponds, and water surface was uniformly open. We therefore assumed that there was no tendency for calling sites to be concentrated on the water surface within 10 cm from the edge in the non-vegetated ponds. Therefore, we conducted a GLM analysis with the site of calling male on the pond water surface (water surface within 10 cm from the shoreline = 1, water surface farther than 10 cm from the shoreline = 0) as the response variable, observation time (daytime = 1, night = 0), pond type (vegetated pond = 1, non-vegetated pond = 0), and number of observation days (1–7) as explanatory variables, the binomial distribution as the error distribution, and the logit link function as the link function.

All possible combinations of explanatory variables were analyzed for both GLMs, and the AIC minimum model (the best model) was selected for each. For the best model, the significance of the coefficients was determined at the 5% level of p value. Both statistical analyses were performed using R version 4.1.0 (R Development Core Team 2021).

Results

The heat map of the calling site is shown in Figure 2. Non-calling males were hidden in the vegetation on the bank during both day and night, and in most cases only calling males were present in the ponds.

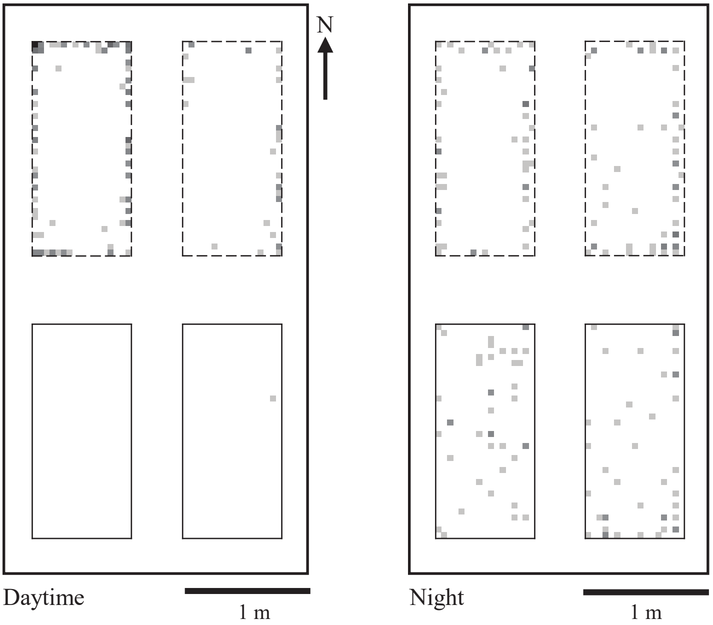

Figure 2. Heatmap of calling sites. The darker the color, the more calling sites that were recorded. The dotted rectangles represent the vegetated ponds, and the solid rectangles represent the non-vegetated ponds, respectively

In the analysis in which the response variable was the pond type selected as the calling site, the model including only the observation time was selected as the best model (Table 1).

In the best model, the regression coefficients of the explanatory variable was positive, and a strong significant association with the response variable was detected. The intercept was not significant. The best model indicated that the vegetated ponds tended to be selected as calling sites in the daytime and non-vegetated ponds tended to be selected as calling sites at night.

In the analysis with the site of calling male on the pond water surface as the response variable, the model including the observation time and the pond type was selected as the best model (Table 2).

Table 1. The results of GLM analysis with “pond type” set as the response variable. The seven models were listed in order of smallest AIC. “Time,” “Day,” and “Depth” represent observation time, number of observation days, and water depth, respectively

Model	Estimated value (SE)							AIC (delta)
	intercept	time	day	depth	time × day	time × depth	day × depth	
1	0.276	4.872***						285.7
	(0.144)	(1.013)						(–)
2	0.438	4.892***	–0.051					287.3
	(0.294)	(1.014)	(0.080)					(1.60)
3	0.329	4.908***		–0.108				287.5
	(0.202)	(1.018)		(0.286)				(1.86)
4	0.922*	4.893***	–0.178	–0.985			0.270	288.3
	(0.426)	(1.018)	(0.111)	(0.597)			(0.163)	(2.63)
5	0.504	4.934***	–0.053	–0.120				289.1
	(0.334)	(1.019)	(0.080)	(0.287)				(3.42)
6	0.452	4.132*	–0.055		0.228			289.1
	(0.296)	(2.083)	(0.081)		(0.605)			(3.44)
7	0.323	17.243		–0.095		–12.515		289.2
	(0.203)	(722.296)		(0.288)		(722.297)		(3.51)

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Table 2. The results of GLM analysis with “the site of calling male on the pond water surface” set as the response variable. The seven models were listed in order of smallest AIC. “Time,” “Day,” and “Pond” represent observation time, number of observation days, and pond type, respectively

Model	Estimated value (SE)							AIC (delta)
	intercept	time	day	pond	time × day	time × pond	day × pond	
1	–0.062	1.555*		2.602***				212.0
	(0.216)	(0.678)		(0.418)				(–)
2	0.282	1.444*	–0.105	1.369			0.435	212.5
	(0.467)	(0.682)	(0.127)	(0.768)			(0.246)	(0.44)
3	0.283	3.198*	–0.105	0.860	–0.631		0.671*	212.5
	(0.467)	(1.544)	(0.127)	(0.850)	(0.457)		(0.332)	(0.47)
4	–0.071	14.637		2.636***		–13.170		213.6
	(0.217)	882.743		(0.426)		(882.744)		(1.58)
5	–0.153	1.545*	0.028	2.608***				214.0
	(0.398)	(0.678)	(0.102)	(0.418)				(1.92)
6	0.270	16.519	–0.104	0.860	–0.637	–13.446	0.693	214.0
	(0.467)	(882.745)	(0.127)	(0.860)	(0.456)	(882.744)	(0.344)	(1.94)
7	0.270	14.608	–0.104	1.402		–13.260	0.436	214.0
	(0.467)	(882.743)	(0.127)	(0.772)		(882.744)	(0.246)	(1.98)

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

In the best model, the regression coefficients of both explanatory variables were positive, and significant associations with the response variable in both explanatory variables were detected. The intercept was not significant in both cases. The best model indicated that the water surface within 10 cm from the shoreline tended to be selected as calling sites in the daytime and in the vegetated ponds.

Discussion and Conclusion

Our results indicate that *P. p. porosus* males tended to select the vegetated ponds as calling sites in the daytime (Figure 2, Table 1). In addition, this experiment also indicated that the water surface within 10 cm from the shoreline tended to be selected as calling sites in the daytime and in the vegetated ponds (Figure 2, Table 2). In the vegetated ponds, the water surface within 10 cm from the shoreline was shaded by vegetation (Figure 1), where males could call while hiding. These results suggest that *P. p. porosus* males select vegetation-shaded water surfaces as calling sites during daytime. Because the snakes, herons and gray-faced buzzards that prey on *P. p. porosus* are diurnal (Kosugi, 1960; Fukada, 1964; Kadowaki, 1992, 1996; Yamada, 1994; Momose et al., 2005; Sakai et al., 2011), the encounter rates with predators are likely to be high during the daytime. Furthermore, conspicuous breeding behaviors, such as vocalizations by male frogs, are known to increase predation risk (Magnhagen, 1991). Since frogs utilize the shade of vegetation as a shelter (Shimoyama, 1989, 1996; Parris, McCarthy, 1999; Sato, Azuma, 2004), we conclude that males select the vegetation-shaded water surfaces as daytime calling sites to attract females under low predation risk condition.

Our findings indicate that *P. p. porosus* males tended to select the non-vegetated ponds as calling sites at night (Figure 2, Table 1). In addition, males tended to select the water surface farther than 10 cm from the shoreline as calling sites at night (Figure 2, Table 2). These results suggest that *P. p. porosus* males select open water surfaces as night calling sites. When males call on open water surface, they are more likely to be detected by predators due to their exposed bodies. On the other hand, calling on the open water surface has some benefits, such as the male's call not being diminished by vegetation and the possibility of using a bimodal (acoustic + visual) signal to attract females, which may enable males to attract females effectively. Because predators such as snakes and birds are less active at night, males are likely to increase their mating success by selecting open water surfaces as night calling sites, which they cannot select in the daytime. However, there is a possibility that the selection of the non-vegetated ponds as a calling site at night might be a result of the overcrowding of the vegetated ponds at night. As we mentioned earlier, maximum of three of *P. p. porosus* males can call on the puddle water surface measuring about 1.5 m^2. Thus, if a total of six males selected the vegetated ponds as calling sites, the vegetated ponds would become unavailable, and some males would have to select the non-vegetated ponds. In contrast, a male that selected the non-vegetated ponds when the number of calling males in the vegetated ponds was less than six would be considered to have selected the non-vegetated ponds out of preference rather than lack of choice. In our experiment, out of a total of 86 cases in which calling males were confirmed in the non-vegetated ponds, the number of calling males in the vegetated ponds was less than six in 73 cases (85%). Furthermore, in 36 cases (42%), calling males were observed in the non-vegetated ponds when there were no calling males in the vegetated ponds. These results suggest that most of the males that selected the non-vegetated ponds at night did so because they preferred non-vegetated ponds over the vegetated ones.

Our results suggest that the presence of vegetation has a major effect on the determination of calling sites in *P. p. porosus* males. Rice planting is one of the human activities that greatly change the distribution of vegetation in paddy fields, and it takes place in middle May (Shimoyama, 1996) or early June (Inoue, 1979; Shimoyama, 1989). Since the breeding season of *P. p. porosus* is from late April to July (Matsui, Maeda, 2018), males call in each paddy field environment where the vegetation distribution differs greatly before and after rice planting, and the determination of the calling site could be influenced by rice planting. For example, the water surface in a paddy field before rice planting is completely devoid of vegetation, and vegetation generally exists only on the banks. Therefore, in the paddy field before rice planting, calling males would concentrate on the water surface near the banks for vegetation cover during daytime, and avoid the water surface near the bank at night. On the other hand, since rice (vegetation) is widely present in the paddy fields after rice planting, daytime calling sites are expected to be dispersed throughout the paddy fields in contrast to before rice planting.

Our results suggest that choice of calling sites by *P. p. porosus* males depends on whether it is daytime or night, because of differences in predation risk between daytime and night. This behavior enhances their survival rate and mating success. In the hylid, *H. squirella*, male frogs calls from deep within vegetation under bright conditions, such as on a full moon night, when it is most vulnerable to predators, and increases the proportion of calling in open sites under dark conditions (Taylor et al., 2007). The results of this previous study are consistent with those of our study in that male frogs select different calling sites depending on environmental conditions. The behavior of selecting different calling sites depending on the environmental conditions, causes the male frogs to incur time and energy costs in searching for a suitable calling site for each situation and moving between calling sites. However, the benefits of such behavior are expected to exceed the costs, and the acquisition of a calling site suitable for each situation is expected to increase the fitness of the males. In the present study, we investigated the selection of calling sites by male frogs in a semi-natural environment. Further studies are necessary to clarify the relationship between calling sites, predation risk, and attractiveness to females in the natural environment will further enhance our understanding of male breeding behavior in frogs.

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