Current Herpetology 40(2): ???–???, August 2021 doi 10.5358/hsj.40.???

Selective Oviposition by Oriental Fire-bellied Toads in Temporally Fluctuating Environments

Seung-Yun BAEK[1,#], Min-Hyun LEE[1,#], Yong-Su KIM[2], Sang-Ryong BAE[2], Uh-Ram SONG[1], and Chang-Ku KANG[2,*]

[1]*Department of Biology, Jeju National University, Jeju 63243, SOUTH KOREA*
[2]*Department of Biosciences, Mokpo National University, Muan 58554, SOUTH KOREA*

Abstract: Selective oviposition is widespread in anurans because it significantly affects the survivorship of their offspring, especially when environmental conditions are heterogeneous and potentially unfavorable. In the present study, we aimed to determine whether female oriental fire-bellied toads (*Bombina orientalis*) selectively lay eggs to increase their progeny's survival. We studied the Jeju Island population because the streams on this island are ephemeral, so the timing and site of egg-laying can be important for the survival of their progeny. We surveyed all pools in a specific area of an ephemeral stream for two years to determine whether female *B. orientalis* selectively lay eggs in certain pools to increase their progeny's survival. The characteristics of pools in our study sites varied especially in size that ranged from 0.01 to 36 m^2 in surface area. We found that female *B. orientalis* avoid laying eggs in very small pools where the risk of desiccation or over-heating of water is high. However, unexpectedly, they also avoided large pools and primarily laid eggs in the pools that are not very small or large. In terms of timing, egg-laying took place in association with the timing of rain: the number of pools with egg clutches decreased as the number of days since the last rainfall increased. Females also avoided laying eggs in pools that were already occupied by tadpoles. Field experiments demonstrated that the degree of cannibalism on eggs by conspecific tadpoles is intense in this species. These findings collectively indicate that *B. orientalis* that live in a fluctuating environment show complicated oviposition behavior that mediate both desiccation and cannibalism risks.

Key words: Anurans; *Bombina orientalis*; Cannibalism; Desiccation; Site-selection

Introduction

Adaptive traits that enable animals to cope with temporal changes in the biotic and abiotic conditions should be favored by natural selection (Scheiner, 2016). This sort of adaptation would especially benefit species living in highly fluctuating environments because this influences their fitness not only by increasing their own survival but also by boosting the performance and survival of their progeny (Higashiura, 1989; Sadeh et al., 2009; Pintar and Resetarits, 2017). Thus, females often make strategic reproductive

* Corresponding author.
E-mail address: changkukang@mokpo.ac.kr
#These authors contributed equally to this work.

decisions that increase their fitness. For example, females of many oviparous species select suitable sites for oviposition to enhance offspring survival (Blaustein and Kotler, 1993; Encalada and Peckarsky, 2006; Refsnider and Janzen, 2010).

Selective oviposition is widely recognized in anurans (Spieler and Linsenmair, 1997; Kloskowski, 2020). The main biotic factors affecting oviposition choice include avoiding predators, cannibalism, and competition (Blaustein, 1999; Matsushima and Kawata, 2005; Lin et al., 2008). Predation is a ubiquitous problem for anuran eggs/tadpoles, therefore, females often lay eggs where predation is less likely (Magnusson and Hero, 1991; Kats and Sih, 1992; Buxton et al., 2017). Tadpoles of many species often show cannibalistic behaviors (usually larger tadpoles cannibalize smaller ones and/or eggs), which also affect female oviposition strategies (Crump, 1992; Sadeh et al., 2009; Buxton and Sperry, 2017). Frogs often avoid laying eggs where conspecific cues exist (Dillon and Fiaño, 2000; von May et al., 2009; Schulte et al., 2011), but this behavior does not appear to be universal (Rudolf and Rödel, 2005; Rojas, 2014). There is also another strategy, shown by the wood frog, *Rana sylvatica*, which synchronizes the timing of egg-laying with that of conspecifics so that tadpoles vary only slightly in size, consequently reducing the risk of cannibalism (Petranka and Thomas, 1995). Some species exploit cannibalistic behaviors to feed their own young. The Amazonian poison frogs, *Dendrobates ventrimaculatus*, occasionally offer their fertilized eggs as food to their tadpoles as desiccation risk increases to stimulate tadpole growth (Poelman and Dicke, 2007).

Abiotic factors also affect female oviposition behaviors (Seale, 1982; Skidds et al., 2007). Because both eggs and tadpoles experience higher survival rates under stable aquatic conditions, they need to avoid exposure to drought conditions (Socci et al., 2005). Many anuran species living in ephemeral pools indeed selectively lay eggs in pools with a high water-holding capacity, where the risk of desiccation is low (Semlitsch, 1987; Rudolf and Rödel, 2005). Often, multiple biotic and abiotic factors jointly affect female choice (Rudolf and Rödel, 2005). For example, *Hoplobatrachus occipitalis* females choose oviposition sites where the risks of both cannibalism and desiccation are low (Spieler and Linsenmair, 1997).

In this study, we investigated the oviposition behavior of the oriental fire-bellied toad, *Bombina orientalis*, on Jeju Island, South Korea. The Jeju Island population has diverged from mainland populations in a number of behavioral and morphological traits because of differences in both predation risk and habitat structure (Kang et al., 2017). Jeju Island's natural habitat is particularly suitable for studying oviposition behavior of the population for several reasons. Unlike in mainland habitats, where streams flow continuously during the breeding season, Jeju Island habitats consist of ephemeral streams, which flow only briefly during and following a period of rain, therefore, the oviposition sites (pools) are distributed patchily (see Fig. 1a). Consequently, the pools' size and other abiotic conditions vary. Some of these pools are at a risk of desiccation when there are consecutive non-rainy days, and occasional flooding occurs after heavy rain. There are many small isolated pools that contain a restricted quantity of organic matter for the tadpoles, which increases the potential risk of cannibalism. Under these heterogeneous and fluctuating environmental conditions, the number of available oviposition sites and their suitability change continuously; therefore, offspring survival could depend largely on the choice of oviposition site and timing of oviposition.

Specifically, we aimed to answer three main questions: (1) Do females selectively lay eggs in pools where the risk of desiccation is low? (2) Do females selectively lay eggs in pools where the risk of cannibalism by conspecific tadpoles is low? (3) Do females adjust their timing of egg-laying when the risk of desiccation and/or flooding can be minimized? Addi-

FIG. 1. (a) A photo of the study site in a non-rainy day. Small isolated pools are distributed in a patchwork. (b) A photo of the same location in heavy rain.

tionally, we empirically tested the occurrence and the degree of egg cannibalism by conspecific tadpoles to determine the importance of oviposition site selection in reducing cannibalism.

MATERIALS AND METHODS

Description of the habitat and study species

The study was conducted within Bang-Cheon stream in Jeju Island, South Korea (33°27'35" N, 126°33'57" E). It has an annual mean temperature of 15.8°C and an annual rainfall of 1,497 mm. The rainfall predominantly occurs between May and September. The mean temperature remains consistently high during the breeding season, ranging from 20 to 30°C (KMA, 2019). The basalt layers covering most Jeju Island drain surface water quickly. As a consequence, most of the streams are ephemeral (i.e., no water flows on non-rainy days), consisting of pools that are isolated from each other on non-rainy days, whereas large volumes of water flow during rain (Fig. 1). The pools were characterized as follows. There were large number of patchy pools close to each other that differ in size (the surface area of pools varied from ca. 0.01 to 36 m^2; the depth of pools varied from 1.5 to 60 cm). Most of the pools were completely separated during non-rainy days (thus tadpoles were unable to move among pools), and the distance among pools varied but usually within several meters (see Fig. 1a). The pools' spatial positions did not change before and after rain, with a few exceptions after heavy flooding, but the number of available pools changed throughout the survey period because of desiccation.

Bombina orientalis is a semi-aquatic frog species that is distributed across South Korea, northern-east China, and adjacent parts of Russia. The reproductive period is long (from May to September), and females lay eggs continuously with a few weeks interval. Cannibalism among tadpoles has been observed (Kang, personal observations).

Field survey

All protocols were approved by the Institutional Animal Care and Use Committee (MNU-IACUC-2019-008). To characterize the spawning patterns of *B. orientalis*, we monitored all pools within a specific area (covering approximately 100 m distance along a stream) for the presence of eggs and tadpoles at regular intervals (every four days in 2018, every two days in 2019) over two years. We surveyed 162 pools in July–August 2018 and 216 pools in May–June 2019. Before beginning the field survey each year, we identified all the pools in the study area and assigned an identification number to each. We visited the pools between 0800 and 1200 h on each survey day unless it rained; in which case, we conducted the survey the day after rain: due to the occurrence and potential risk of flooding, it was impossible to visit the streams in the rain.

On each survey day, we carefully checked the pools for the presence of egg clutches and tadpoles. We examined underwater areas by removing pebbles/stones and sweeping the pool using a small mesh basket (1.2 mm mesh size) to be certain that we did not miss any hidden eggs or tadpoles. We also recorded egg clutches and tadpoles of other anuran species (mostly *Rana dybowskii* and *Hyla japonica*). It was difficult to estimate whether egg clutches were deposited from a single female or multiple females. Instead, we used a binary category for the presence of egg clutches. During each survey, we also recorded whether each pool was dry or not.

For each pool, we estimated the volume and canopy cover directly overhead. Pool volume changed daily depending on the timing of rain and the degree of water evaporation. We assumed that the daily water volume change was similar across all the pools, so we estimated the volume of each once, just after rainfall when they all contained water. To estimate the volume of each pool, which was often highly irregular three-dimensional, we first measured the surface area using a photographic method: we photographed each pool with a ruler next to it and measured the surface area of each pool using ImageJ 1.80 (National Institutes of Health, Maryland, USA). We then measured the depth of the deepest part of each pool and multiplied the surface area by the depth. We used this value as a proxy for each pool's actual volume. The canopy cover above each pool was also estimated using the photographic method. We placed a camera (IPhone6, Apple Inc, California, USA) 10 cm above each pool, facing directly upwards, and took a photograph. Then we estimated the canopy cover (the proportion of plant cover in each image) using ImageJ. The canopy cover of pools varied from 0 to 85%. The camera's angular field of view was 73°.

Testing the occurrence of egg cannibalism

We conducted two experiments (field and controlled experiments) to confirm the occurrence of cannibalistic behavior and quantify the degree of egg cannibalism in June-July 2019, just after the completion of field survey. In the field experiment, we located two similar-sized natural pools in close proximity (<10 m) and used them as a paired group. First, we removed all eggs and tadpoles in the pools. Then we put 20 eggs in both pools and added 20 tadpoles (Gosner stages 21–25; Gosner, 1960) in only one of the paired pools. The collected eggs and tadpoles were put together in containers separately and used for the experiment randomly. We replicated this trial with 30 different pairs of pools and measured the survival of eggs after 24 hours. We determined which pool within each pair to add tadpoles by tossing a coin.

During this field experiment, we removed any eggs and tadpoles present in the pools before running the experiment. Lingering chemical cues could have affected tadpole behavior, and the disappearance of eggs may not be solely explained by cannibalism but also by predators (Crossland and Shine, 2010). To remove these potential confounding effects, we conducted an additional controlled experiment that removed the effect of external predators and chemical cues. In the controlled experiment, we created two similar-sized artificial pools (approximately 35×30×5 cm) outdoors, covered them completely using a mosquito net and filled them with water collected from the same natural pools. Then we put 15 eggs in both pools, added 20 tadpoles in one of the pools, and measured the eggs' survival after 24 hours. We replicated this trial 15 times by alternating the position of the pool we added tadpoles. In both experiments, we used each tadpole and egg only once and replaced them for every trial. We released all tadpoles and surviving eggs after the experiments.

Data analysis

To evaluate whether the pools' abiotic conditions affected the female' choice of oviposition site, we fitted generalized linear models (binomial error structure) and used three physical properties of each pool as predictor variables: 1) the proportion of time that each pool was found to be dry during the survey, 2) the estimated volume of each pool, and 3) the canopy cover of each pool. We then generated a binary variable, recording whether eggs were found in each pool at least once during the survey period or not, and used this as the response variable. Data exploration suggested a non-linear relationship between pool volume and the presence of eggs; therefore, we fitted polynomial predictors for pool volume. We included quadratic terms for the analysis because the statistical model using quadratic terms showed the lowest Akaike Information Criterion. We log-transformed the estimated pool volume before analysis.

We also tested whether the risk of desiccation affected female choice in the following way. We counted the number of times where a pool was dry and divided this number by the total number of survey dates. Then, we fitted a generalized linear mixed model, using this proportion as an explanatory variable. For the response variable, we generated a binary variable whether eggs were found in each pool at least once during the survey or not and used it. The survey year was set as an additional predictor. We additionally fitted a linear regression to test whether the estimated pool volume (predictor) predicts the probability that each pool was dry in each survey date (response). To test whether desiccation risk affected oviposition choice, we fitted a logistic regression using this dry probability as a predictor and the proportion of time that each pool was found with egg clutches as a response variable.

Testing whether frogs select oviposition sites without tadpoles required several steps in data analysis because the number of available pools changed continuously during the survey. First, we calculated the frequency of available (i.e., non-dried) pools and the pools with tadpoles for each survey. Then, we pooled these frequencies across the survey. Using these data, we estimated the expected frequencies of pools with and without egg clutches if female frogs laid their eggs randomly, regardless of the presence of tadpoles. We then generated a 2×2 contingency table, using the four frequencies (expected and observed frequencies of pools with egg clutches in either tadpole-free and tadpole-present pools) and performed a chi-square test. Pooling across all the survey dates was unavoidable because the number of egg clutches found in each survey was often too low (often <3) to estimate the expected frequencies for each date.

To determine whether the timing of rain correlates with the timing of egg laying, we calculated how many surveys had been carried out since the last rain for each survey period and used a Spearman correlation test to assess whether there was a correlation between time since the last rainfall and the number of egg clutches found during each survey. We analyzed the count of the survey, not the actual number of days passed because frequent rain often constrained regular survey, thus the number of days passed since the last rain differed among survey dates. Therefore, having the count of survey on x-axis more directly shows the relationship. We used paired t-tests to compare the number of surviving eggs between the paired pools (tadpole-free vs. tadpole-added) to analyze egg-cannibalism experiment data. We used R for all statistical analyses (R Core Team, 2014).

Results

We found 19 egg clutches in 2018 and 367 egg clutches in 2019. Thus, our results were mainly affected by the trends observed in 2019. Female frogs preferred to lay their eggs in mid-sized pool (among the surveyed pools; the estimated peak value in Fig. 2a corresponds to ca. 0.06 m^3 pool), avoiding both relatively small and large pools (Fig. 2a; quadratic: $z=-3.955$, $P<0.001$, linear: $z=4.017$, $P<0.001$). Not surprisingly, there was a negative correlation between the estimated pool volume and the proportion of time that each pool was dry ($r=-0.31$, $t_{355}=-6.21$, $P<0.001$). Egg clutches were more likely to be found in pools with a lower risk of desiccation (Fig. 2b; $z=-4.659$, $P<0.001$). Canopy coverage had no effect on female egg-laying choice ($z=-0.560$, $P=0.575$).

The numbers of egg clutch found in the presence or absence of tadpoles deviated significantly from the numbers expected by random chance (Fig. 3; $\chi^2_1=43.577$, $P<$

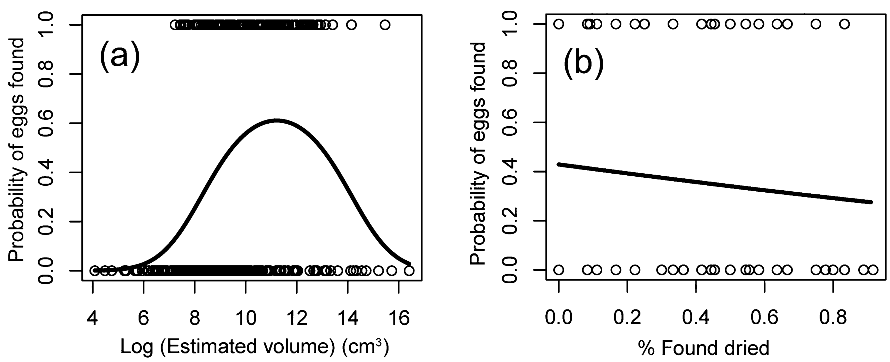

FIG. 2. Binary fitted line plots showing the relationship between pool properties and the probability that egg clutches were found. (a) The relationship between the volume of each pool and the probability that egg clutches were found at least once during the survey in that pool. (b) The relationship between the proportion of the time that each pool was found dry during the survey and the probability that egg clutches were found at least once during the survey in that pool.

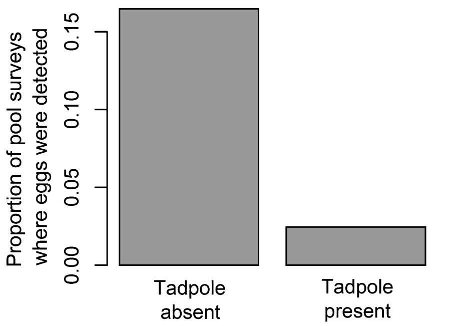

FIG. 3. The proportions of pools containing egg clutches when tadpoles were present or absent.

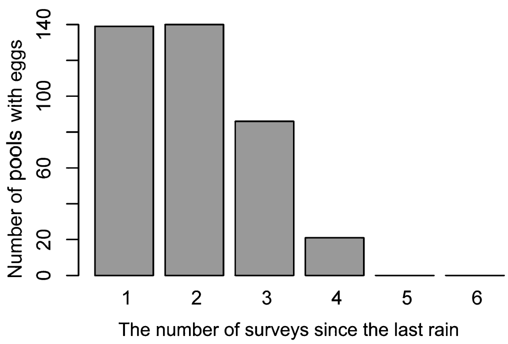

FIG. 4. The relationship between the number of surveys conducted since the last rainfall and the number of egg clutches found.

0.001): eggs were almost exclusively found in pools without conspecific tadpoles. We found 378 clutches out of 2,294 surveys of pools where tadpoles were never found (16.5%; pools summed across our survey dates as explained in methods). In contrast, only eight clutches were found out of 326 surveys of pools where tadpoles were found at least once (2.5%). In terms of egg-laying timing, there was a significant negative correlation between the number of egg clutches found and the number of surveys conducted since the last rainfall (Fig. 4; S=67.46, rho=–0.93, P= 0.02). This shows that most of the egg-laying occurred within several days after rain and that females did not lay eggs when there were consecutive non-rainy days.

In the egg-cannibalism experiments, egg survival was significantly lower in tadpole-added pools than tadpole-free pools in both field (Fig. 5; 20% survived in tadpole-added pools while 96% survived in tadpole-free pools; $t_{29}=13.626$, $P<0.001$) and controlled experiments (25% vs. 100%; $t_{14}=12.87$, $P<0.001$).

DISCUSSION

Our results demonstrate that female *B.*

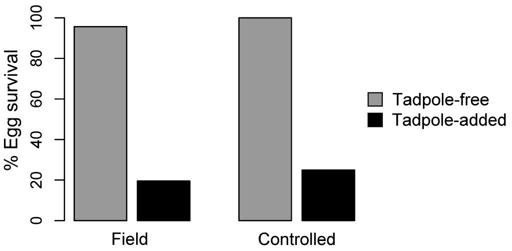

FIG. 5. Egg survivorship comparisons in the field (n=30 paired pools) and the controlled (n=15 pairs) egg-cannibalism experiments.

orientalis on Jeju Island selectively lay their eggs in response to both desiccation and cannibalism risk. Females avoided laying eggs in pools where conspecific tadpoles were already present. This apparently allows females to avoid the risk of egg-cannibalism and potentially decreases intraspecific competition. Considering the intense cannibalism rates demonstrated in the experiments, avoiding cannibalism seems to be the primary benefit of this selective oviposition rather than avoiding competition. Females also avoided laying eggs in pools that were either too small or large. In addition, egg clutches were found exclusively within several days after rain, while there were no eggs found when no rainfall had occurred over multiple days. These findings suggest that the avoidance of desiccation affected timing of female oviposition. Intriguingly, females also avoided large pools, even though the potential risk of desiccation was low. One explanation for this may be that the water temperature of larger pools does not fluctuate much compared to smaller pools due to their large volume, thus maintaining lower temperatures during the breeding season. Anuran egg/tadpole development speed depends on temperature, with development being accelerated under warmer conditions (Álvarez and Nicieza, 2002). In fluctuating environments, such as in Jeju Island habitats, rapid development may be desirable because, if they leave the pool early, the progeny can reduce the potential risks associated with isolated pools, such as cannibalism, food limitation, flooding, or desiccation. Thus, female *B. orientalis* may have evolved to avoid laying eggs in cold water (which is more likely in larger pools), where the growth of eggs/tadpoles is slow which may explain why female *B. orientalis* avoiding large pools to lay eggs. Another possibility is that larger pools may be more vulnerable to predators. However, we find this possibility less likely because aquatic predators are absent or scarce in our study site (see below), and predation pressure from terrestrial predators may be neutral or even higher in smaller pools than larger pools because there is less space to retreat and fewer refuges to use (Carver et al., 2010). The reason why females did not prefer to lay eggs in larger pools remains to be determined.

Though female preference is influenced by some factors but not others, our results overall suggest that mediating the risk of both desiccation and cannibalism affected their choice. Still, it is not clear whether female oviposition behavior was also affected by predation, a well-known factor that has shaped selective oviposition in other anuran species (Rudolf and Rödel, 2005). However, we consider that predation risk did not significantly affect females' egg-laying site selection in our study site because, in Jeju Island's natural habitats, most pool volumes are not large enough for larger aquatic predators, and frequent flooding prevents from them living permanently in pools. This excludes the possibility of aquatic predation by fish. Indeed, we did not observe any fish in the pools during our surveys (personal observations by all authors). The risk from terrestrial predators or predators that can tolerate ephemeral pools (such as odonate naiads) is difficult to estimate. It is also possible that females avoid laying eggs in large pools because invertebrate predators may be more likely to occur in such pools. It is also not clear whether egg-laying just after rain would help avoid the risk of flooding. Considering it is practically impossible to predict when flooding will occur, desiccation, rather than flooding, is likely to be the main factor that affects timing of female egg laying because the risk of desiccation can be predicted both spatially and temporally using environmental cues.

In summary, our results suggest that female *B. orientalis* on Jeju Island show adaptive oviposition behaviors that mediate the risk of both desiccation and cannibalism. The heterogeneity in water holding potential and cannibalism risk among pools seem to have shaped this parental behavior. It has been widely recognized that female frogs selectively choose egg-laying sites to increase their offspring's survival (Kats and Sih, 1992; Rudolf and Rödel, 2005). Our study provides an additional line of evidence that female anurans experiencing ephemeral conditions show selective oviposition behaviors.

Acknowledgments

This study was funded by the National Research Foundation of Korea (NRF-2019R1C1C1002466).

Literature Cited

Álvarez, D. and Nicieza, A. G. 2002. Effects of temperature and food quality on anuran larval growth and metamorphosis. *Functional Ecology* 16: 640–648.

Blaustein, L. 1999. Oviposition site selection in response to risk of predation evidence from aquatic habitats and consequences for population dynamics and community structure. *In*: S. P. Wasser (ed.), *Evolutionary Theory and Processes Modern Perspectives.* Kluwer Academic Publishers, Dordrecht.

Blaustein, L. and Kotler, B. P. 1993. Oviposition habitat selection by the mosquito, *Culiseta longiareolata*: effects of conspecifics, food and green toad tadpoles. *Ecological Entomology* 18: 104–108.

Buxton, V. L. and Sperry, J. H. 2017. Reproductive decisions in anurans: a review of how predation and competition affects the deposition of eggs and tadpoles. *Bioscience* 67: 26–38.

Buxton, V. L., Ward, M. P., and Sperry, J. H. 2017. Frog breeding pond selection in response to predators and conspecific cues. *Ethology* 123: 397–404.

Carver, S., Spafford, H., Storey, A., and Weinstein, P. 2010. The roles of predators, competitors, and secondary salinization in structuring mosquito (Diptera: Culicidae) assemblages in ephemeral water bodies of the wheatbelt of Western Australia. *Environmental Entomology* 39: 798–810.

Crossland, M. R. and Shine, R. 2010. Cues for cannibalism: cane toad tadpoles use chemical signals to locate and consume conspecific eggs. *Oikos* 120: 327–332.

Crump, M. L. 1992. Cannibalism in amphibians. *In*: M. A. Elgar, and B. J. Crespi (eds.), *Cannibalism: Ecology and Evolution among Diverse Taxa.* Oxford University Press, New York.

Dillon, M. E. and Fiaño, J. 2000. Oviposition site selection by the túngara frog (*Physalaemus pustulosus*). *Copeia* 2000: 883–885.

Encalada, A. C. and Peckarsky, B. L. 2006. Selective oviposition of the mayfly *Baetis bicaudatus*. *Oecologia* 148: 526–537.

Gosner, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* 16: 183–190.

Higashiura, Y. 1989. Survival of eggs in the gypsy moth *Lymantria dispar*. II. Oviposition site selection in changing environments. *Journal of Animal Ecology* 58: 413–426.

Kang, C., Sherratt, T. N., Kim, Y. E., Shin, Y., Moon, J., Song, U., Kang, J. Y., Kim, K., and Jang, Y. 2017. Differential predation drives the geographical divergence in multiple traits in aposematic frogs. *Behavioral Ecology* 28: 1122–1130.

Kats, L. B. and Sih, A. 1992. Oviposition site selection and avoidance of fish by streamside salamanders (*Ambystoma barbouri*). *Copeia* 1992: 468–473.

Kloskowski, J. 2020. Better desiccated than eaten by fish: distribution of anurans among habitats with different risks to offspring. *Freshwater Biology* 2020: 62 2124–2134.

KMA, 2019. Automatic Weather Station (AWS). Korea Meteorological Administration, http://www.weather.go.kr/weather/observation/aws_ table_popup.jsp (accessed 15 January 2020)

LIN, Y. S., LEHTINEN, R. M., AND KAM, Y. C. 2008. Time- and context-dependent oviposition site selection of a phytotelm-breeding frog in relation to habitat characteristics and conspecific cues. *Herpetologica* 64: 413–421.

MAGNUSSON, W. E. AND HERO, J. M. 1991. Predation and the evolution of complex oviposition behavior in Amazon rainforest frogs. *Oecologia* 86: 310–318.

MATSUSHIMA, N. AND KAWATA, M. 2005. The choice of oviposition site and the effects of density and oviposition timing on survivorship in *Rana japonica*. *Ecological Research* 20: 81–86.

PETRANKA, J. W. AND THOMAS, D. A. G. 1995. Explosive breeding reduces egg and tadpole cannibalism in the wood frog, *Rana sylvatica*. *Animal Behavior* 50: 731–739.

PINTAR, M. R. AND RESETARITS, W. J. 2017. Out with the old, in with the new: oviposition preference matches larval success in Cope's Gray Treefrog, *Hyla chrysoscelis*. *Journal of Herpetology* 51: 186–189.

POELMAN, E. H. AND DICKE. M, 2007. Offering offspring as food to cannibals: oviposition strategies of Amazonian poison frogs (*Dendrobates ventrimaculatus*). *Evolutionary Ecology* 21: 215–227.

R CORE TEAM. 2014. *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

REFSNIDER, J. M. AND JANZEN, F. J. 2010. Putting eggs in one basket: ecological and evolutionary hypotheses for variation in oviposition-site choice. *Annual Review of Ecology, Evolution, and Systematics* 41: 39–57.

ROJAS, B. 2014. Strange parental decisions: fathers of the dyeing poison frog deposit their tadpoles in pools occupied by large cannibals. *Behavioral Ecology and Sociobiology* 68: 551–559.

RUDOLF, V. H. W. AND RÖDEL, M. O. 2005. Oviposition site selection in a complex and variable environment: the role of habitat quality and conspecific cues. *Oecologia* 142: 316–325.

SADEH, A., MANGEL, M., AND BLAUSTEIN, L. 2009. Context-dependent reproductive habitat selection: the interactive roles of structural complexity and cannibalistic conspecifics. *Ecology Letters* 12: 1158–1164.

SCHEINER, S. M. 2016. Habitat choice and temporal variation alter the balance between adaptation by genetic differentiation, a jack-of-all-trades strategy, and phenotypic plasticity. *The American Naturalist* 187: 633–646.

SCHULTE, L. M., YEAGER, J., SCHULTE, R., VEITH, M., WERNER, P., BECK, L. A., AND LOTTERS, S. 2011. The smell of success: choice of larval rearing sites by means of chemical cues in a Peruvian poison frog. *Animal Behavior* 81: 1147–1154.

SEALE, D. B. 1982. Physical factors influencing oviposition by the woodfrog, *Rana sylvatica*, in Pennsylvania. *Copeia* 1982: 627–635.

SEMLITSCH, R. D. 1987. Relationship of pond drying to the reproductive success of the salamander *Ambystoma talpoideum*. *Copeia* 1987: 61–69.

SKIDDS, D. E., GOLET, F. C., PATON, P. W. C., AND MITCHELL, J. C. 2007. Habitat correlates of reproductive effort in wood frogs and spotted salamanders in an urbanizing watershed. *Journal of Herpetology* 41: 439–450.

SOCCI, A. M., SCHLAEPFER, M. A., AND GAVIN, T. A. 2005. The importance of soil moisture and leaf cover in a female lizard's (*Norops polylepis*) evaluation of potential oviposition sites. *Herpetoloica* 61: 233–240.

SPIELER, M. AND LINSENMAIR, K. E. 1997. Choice of optimal oviposition sites by *Hoplobatrachus occipitalis* (Anura: Ranidae) in an unpredictable and patchy environment. *Oecologia* 109: 184–199.

VON MAY, R., MEDINA-MÜLLER, M., DONNELLY, M. A., AND SUMMERS, K. 2009. Breeding-site selection by the poison frog *Ranitomeya biolat* in Amazonian bamboo forests: an experimental approach. *Canadian Journal of Zoology* 87: 453–464.

Accepted: 24 March 2021