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Abiotic effects on calling phenology of three frog species in Korea

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Calling behavior is often used to infer breeding patterns in anurans. We studied the seasonal and diel calling activities of anuran species in a wetland in central Korea to determine the calling season and to evaluate the effects of abiotic factors on male calling. Acoustic monitoring was used in which frog calls were recorded for a full day, once a week, throughout an entire year. Using acoustic monitoring, we identified three frog species in the study site. Males of *Rana dybowskii* called in late winter and early spring; we thus classified this species as a winter/spring caller. The results of binary logistic regression showed that temperature, relative humidity, and 1-day lag rainfall were significant factors for male calling in *R. dybowskii*. Temperature and relative humidity were important factors for the calling activity of *R. nigromaculata*, whereas 24-h rainfall and 1-day lag rainfall were not significant. Thus, we determined *R. nigromaculata* to be a summer caller independent of weather. In *Hyla japonica*, relative humidity, 24-h rainfall, and 1-day lag rainfall were significant for male calling, suggesting that this species is a summer caller dependent on local rain.

Keywords: acoustic monitoring; calling season; *Hyla japonica*; *Rana dybowskii*; *Rana nigromaculata*

ECOLOGY & POPULATION BIOLOGY

Introduction

Male anurans produce species-specific advertisement calls to attract conspecific, receptive females for mating (Gerhardt and Huber 2002). The calls mediate intraspecific communications such as male-male competition and mate choice. Furthermore, species recognition between closely related sympatric species often depends on differences in call characteristics. Although the function of an advertisement call is generally clear in anurans, the temporal and spatial distribution of calling activity and the factors affecting that distribution remain largely obscure. There are at least five recognized categories of anuran calling behavior in relation to breeding (Saenz et al. 2006): (1) year-round callers, (2) winter/spring callers, (3) summer callers independent of weather, (4) summer callers dependent on local rain, and (5) large rainfall event callers.

Year-round callers are typically found in aseasonal environments where abiotic conditions remain relatively constant throughout the year (Crump 1974). However, year-round callers do occur in seasonal environments with varying rainfall and temperature, depending on season. Winter/spring callers produce advertisement calls in winter and spring when temperatures are low. Ectothermic animals that are active in winter and spring are physiologically adapted to cold water and temperature (John-Alder et al. 1988; Schmidt-Nielsen 1997). Summer callers independent of weather have a prolonged period of breeding (Conant 1988; Saenz et al. 2006). They use permanent water and have relatively long larval periods. The activity of summer callers dependent on local rain is positively associated with rainfall or lags after rainfall (Saenz et al. 2006). The large rainfall event callers typically rely on highly ephemeral sites and large rain events (Saenz et al. 2006). They tend not to have a well-defined breeding season.

Based on intensity and duration of breeding, anurans may be classified as either explosive or prolonged breeders (Wells 1977; Oseen and Wassersug 2002; Prado et al. 2005). Explosive breeders typically form dense aggregations and engage in scramble competition in which males physically compete with each other for access to females; the females arrive synchronously at breeding sites. In prolonged breeders, the arrival of females is less synchronized, and males are generally stationary, producing advertisement calls. Females of prolonged breeders are regarded to have more opportunities for mate choice than do females of explosive breeders. The winter/spring callers and large rainfall event callers are regarded as explosive breeders, whereas year-round callers and both types of summer callers are prolonged breeders.

Here, we used acoustic monitoring to study the calling behavior of anuran populations in a wetland site in central Korea. To understand seasonal and diel calling patterns of all anuran species found in that site, we conducted 24 hours of acoustic monitoring, once a week, throughout a year. Furthermore, we evaluated the effects of abiotic factors such as temperature, humidity, and rainfall on male calling in frog species. Acoustic monitoring is ideal for studying the calling activity of anuran populations. Because sampling can

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be conducted for extended periods of time with minimal disturbance, and it yields a permanent recording, acoustic monitoring has been successfully implemented for anuran calling surveys (Bridges et al. 2000; Dorcas et al. 2009).

There are at least 13 anuran species in central Korea. Based on previous studies (Yang 2000; Yang et al. 2001), ten species might be found in the study site: *Rana dybowskii*, *R. nigromaculata*, *R. plancyi*, *R. amurensis*, *R. huanrensis*, *Hyla japonica*, *H. suweonensis*, *Kaloula borealis*, *Bombina orientalis*, and *Bufo gargarizans*. Most of these frog species have one or two well-developed vocal sacs and produce distinctive advertisement calls, ideal for acoustic monitoring. However, *R. plancyi* and *B. orientalis* have no vocal sacs, and their calls are generally short and weak. Using the acoustic monitoring, we expected to easily detect advertisement calls of all but these two species, if these species occur at the study site.

Materials and methods

Study site

The study site (37°24′N, 127°8′E) was located in the city of Seongnam, about 23 km south of Seoul, Republic of Korea. Central Korea has a humid continental climate and four distinct seasons: winter, spring, summer and autumn (Figure 1). The winter is characterized by freezing temperatures and snow, and the summer is hot and humid, with temperatures regularly exceeding 25 °C. In addition, there may be short rainy seasons, called 'jangma', during the summer when most of the yearly rainfall is concentrated.

Because the study area is a part of the Green Belt, a series of protected forest areas surrounding the capital region, development is restricted in the immediate vicinity. Nonetheless, the study site was just under 100 m away from a residential area and about 160 m away from main roads. Because the study site was located at the base of a mountain with a peak elevation of 414 m, there were occasional hikers passing through near the study site. Right next to the study site, there was also an outdoor nature school where schoolchildren came for outdoor activities during the daytime. However, the study site was protected by fences and a gate and was closed to the public.

The study site is an artificial wetland, including ponds and rice paddies, surrounded by pine and oak trees that are typical of deciduous forests in central Korea. There are four rice paddies, arranged vertically in steps. The rice paddies range in size from about 10 to 35 m^2. In the middle of these rice paddies, there are two artificial ponds with surface areas of 5 and 23 m^2. In winter, the ponds were usually covered with ice, but rice paddies were dry. The ponds and rice paddies were maintained not for food production, but to provide a habitat for fireflies. Thus, agricultural chemicals were strictly prohibited in these artificial wetlands. Although rice seedlings were planted at the beginning of early June, weeds become dominant in the rice paddies by late August.

Acoustic monitoring and data analysis

We conducted weekly acoustic monitoring for one year, beginning 26 May 2009 and ending 18 May 2010. The weekly monitoring typically commenced around 3 pm on Tuesdays and lasted 24 h. Thus, there were 51 24-h recordings for the acoustic monitoring data. We recorded sounds using two Sony PCM D50 digital recorders (Tokyo, Japan) with a sampling rate of 44,100 Hz and a resolution of 16 bits. To increase the dynamic range of recording, the two digital recorders were set to two different levels of recording sensitivity; each recorder was connected to an external omni-directional microphone (Sennheiser ME 62 + K6 powering module; frequency response: 20–20,000 Hz $\pm$ 2.5 dB; Wedemark, Germany). The microphones were fixed in a pistolgrip (MZS20-1 Combo Mount; Sennheiser; Wedemark, Germany) and then covered with a Blimp windscreen (MZW20-1; Sennheiser; Wedemark, Germany). The tips of the microphones were facing directly up. The microphone set was protected by a rain cover (REM-RMAN Rainman Boom Mic Rain Cover; Remote Audio, USA). The microphone set was placed 45cm above the ground on the bank of a rice paddy in the middle of the study site. An instrument shelter ($60 \times 60 \times 60$ cm) placed 50 cm from the ground housed the two digital recorders and batteries to power the system as well as a data logger (8828, AZ instrument Corp. Taichung, Taiwan) to record air temperature and relative humidity. Rainfall data were obtained from a meteorological station in Seongnam, located approximately 4.7 km from the study site. The recording files from acoustic monitoring were analyzed using Cool Edit 2000 (Syntrillium Software Corporation; Phoenix, Arizona, USA). Anuran vocalizations were identified to species. For call identification, we referred to Park and Yang (1997) for *R. nigromaculata*, to Park et al. (1996) for *H. japonica*, and to Y. Jang (unpublished data) for *R. dybowskii*.

Statistical analysis

Each 24-h recording file was divided into 10-min files, and the calling activity of each frog species was scored

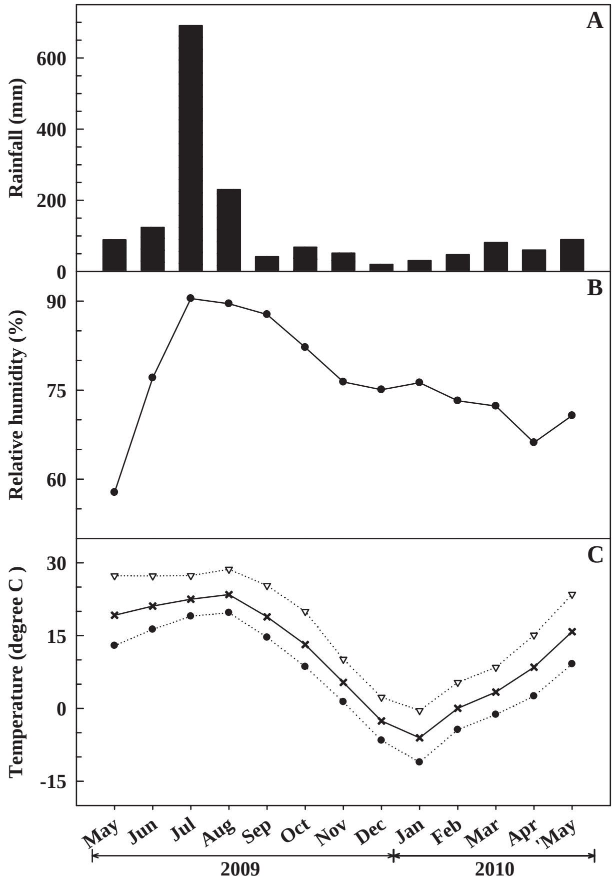

Figure 1. Climatic conditions of the study site: mean monthly rainfall (A), mean monthly relative humidity (B) and mean monthly temperature (C). In addition to mean monthly temperature (×), the means of the daily lowest (●) and highest (∇) temperatures are also shown. The temperature and relative humidity data were recorded from the study site, and the rainfall data were obtained from a meteorological station near the study site.

in a binary fashion (for presence or absence) for each 10-min interval. For example, if there was at least one call of a particular frog species in a given 10-min period, the calling activity for that species was scored '1' for that 10-min interval; if not, it was scored '0'. In an hour, the maximum value of the calling activity for a given frog species was 6, and the minimum value was 0.

We explored the relationship between calling activity and two abiotic factors, temperature and relative humidity, by comparing these factors between times of calling and non-calling using *t*-tests. One-way ANOVA was used to determine whether calling activities of the three species differed with respect to temperature and relative humidity. We used binary logistic regression to test for the hypothesis of no relationship between calling activity and abiotic factors. Calling activity was binary, indicating whether a given frog species sang (1) or did not sing (0) in each 10-min interval. Thus, we used a binominal distribution with a probit link function in the binary logistic regression. Abiotic factors included temperature, relative humidity, 24-h rainfall, and 1-day lag rainfall. The 24-h rainfall was the accumulated rainfall for 24 h prior to a given time interval, and 1-day lag rainfall was the accumulated rainfall between 24 and 48 h prior to a given time interval. We used R 2.11.0 (R Development Core Team 2010) for the analysis of binary logistic regression and SPSS 11 (SPSS Inc.; Chicago, Illinois, USA) for all other statistical analyses.

Results

Seasonal and diel calling patterns

Using acoustic monitoring, we identified three frog species in the study site. *R. dybowskii* called between late February and mid March (Figure 2). Both *R. nigromaculata* and *H. japonica* started calling in the first week of May. *R. nigromaculata* called until early June, whereas *H. japonica* called until early August. There were no frog calls between September and the following January. In this study, the calling seasons of *R. dybowskii*, *R. nigromaculata* and *H. japonica* were determined to be from 23 February to 16 March, from 4 May to 3 June, and from 4 May to 4 August, respectively.

The calling activity of *R. dybowskii* was explosive in that it was concentrated mostly on one recording day (Figure 2). Unlike *R. dybowskii*, calling activities of *R. nigromaculata* and *H. japonica* were spread out throughout their respective calling seasons. The daily distribution of calling activity was bimodal in *R. dybowskii* (Figure 3). The first peak occurred between 1 and 2 pm, and the other peak was between 6 and 11 pm. *R. dybowskii* rarely sang after midnight. By contrast, the calling activities of *R. nigromaculata* and *H. japonica* started around 7 or 8 pm and lasted throughout the night. There was a burst of calling in the morning in *R. nigromaculata*.

Abiotic effects on calling activity

R. dybowskii called at lower temperatures than did *R. nigromaculata* and *H. japonica* (Figure 4). In fact, males of *R. dybowskii* called sometimes when air temperatures were below 0 °C. The temperature ranges of calling were generally overlapping for *R. nigromaculata* and *H. japonica*. Both *R. nigromaculata* and *H. japonica* called at higher relative humidity than *R. dybowskii* did. Furthermore, the ranges of relative humidity were narrower in *R. nigromaculata* and *H. japonica* than in *R. dybowskii* (Figure 4).

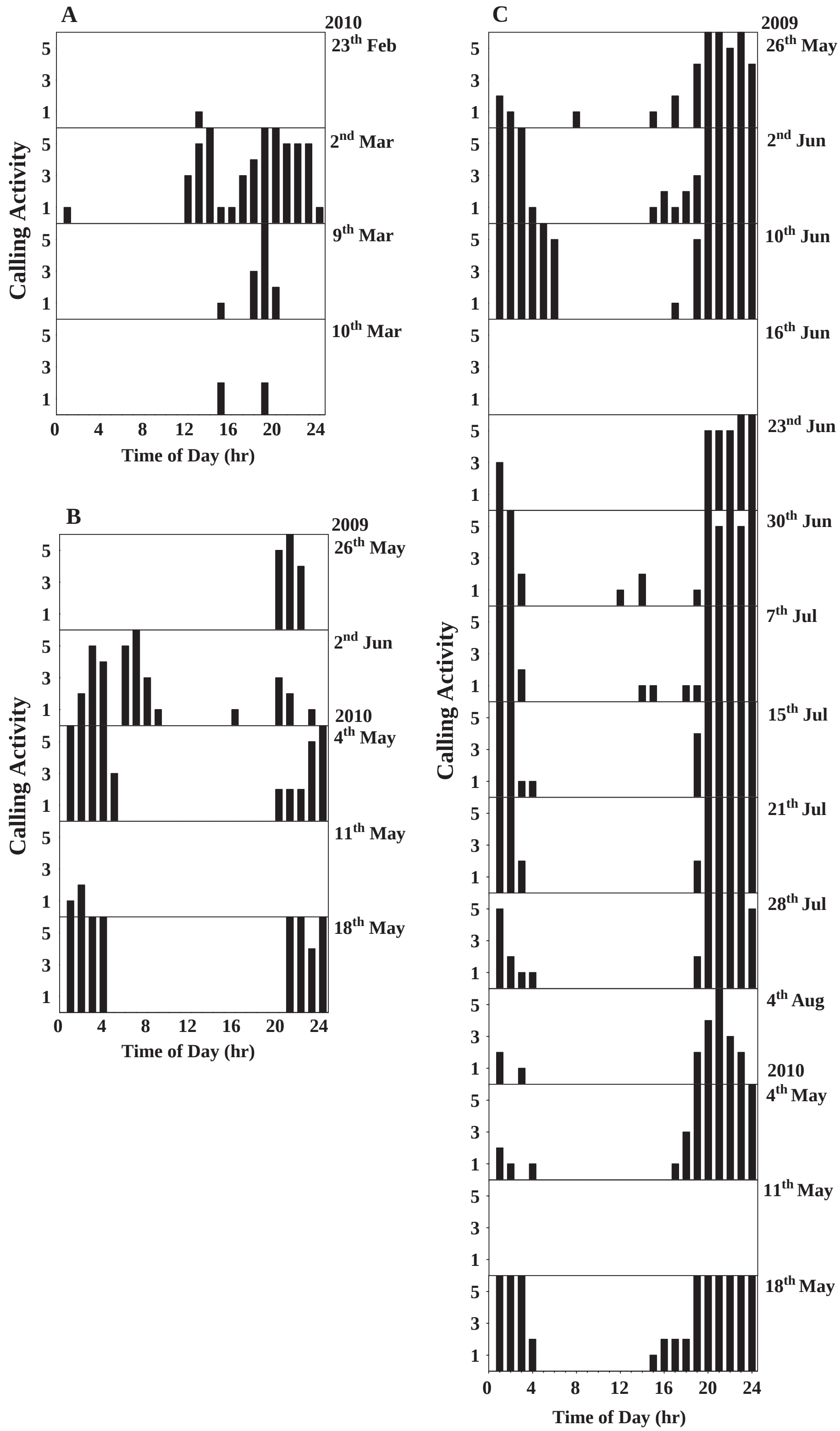

Figure 2. Diel calling activities for *R. dybowskii* (A), *R. nigromaculata* (B), and *H. japonica* (C). Acoustic monitoring was conducted once a week from 26 May 2009 to 18 May 2010. Each monitoring period lasted for 24 h. There were heavy rains on two days,16 June 2009 and 11 May 2010, and no frog calls were recorded on these two days.

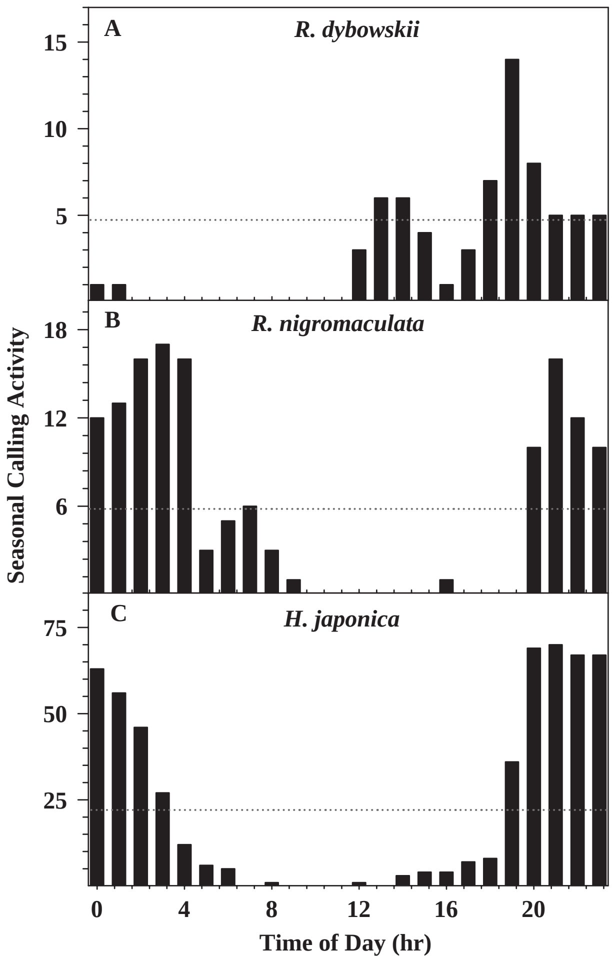

Figure 3. Seasonal calling activity for *R. dybowskii* (A), *R. nigromaculata* (B), and *H. japonica* (C). Seasonal calling activity was the cumulative calling activity of the entire calling season. The sample size was 69 for *R. dybowskii*, 108 for *R. nigromaculata*, 494 for *H. japonica*. The dotted line indicates one third of the peak calling activity for each species.

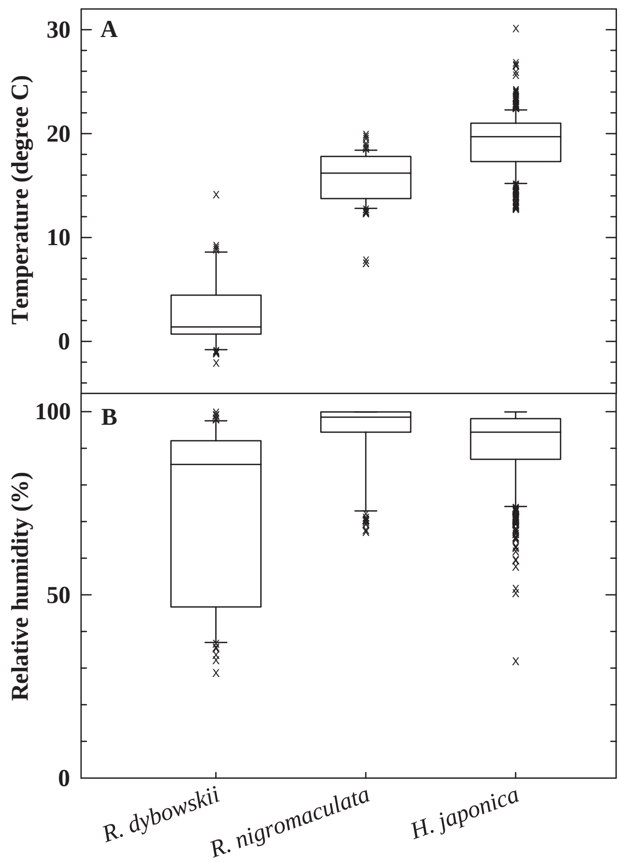

Figure 4. Box plots showing distributions of temperature (A) and relative humidity (B) for the calling activity during the entire calling season. Top, middle, and bottom lines of the boxes indicate 75th percentile, median, and 25th percentile, respectively. The upper and lower whiskers indicate 90th and 10th percentiles, respectively. X indicates an outlier.

There were significant differences in temperature and relative humidity between times of calling and non-calling in *R. nigromaculata* and *H. japonica* (Table 1). That is, during their respective calling seasons, the times that these two frog species sang had lower temperatures and higher relative humidity than the times they did not sing. In *R. dybowskii,* there was a significant difference in air temperature between times of calling and non-calling, but there was no significant difference in relative humidity between times of calling and non-calling. During the *R. dybowskii* calling season, times of calling had higher temperatures than times of non-calling. The three frog species' calling activity differed significantly in temperature (one-way ANOVA; $F_{2,670} = 1020.02$, $P < 0.001$) and relative humidity (one-way ANOVA; $F_{2,670} = 60.14$, $P < 0.001$) for calling. Post hoc comparisons showed that all species pairs' calling periods were significantly different with respect to temperatures and relative humidity

The results of binary logistic regression revealed that temperature, relative humidity, and 1-day lag rainfall were significant factors for male calling in *R. dybowskii* (Table 2). In *R. nigromaculata*, temperature and relative humidity were significant factors for male calling, whereas two rainfall factors were not. In *H. japonica*, both rainfall factors and relative humidity were significant for male calling. Unlike *R. dybowskii* and *R. nigromaculata*, however, *H. japonica* did not respond significantly to temperature.

Discussion

Using acoustic monitoring, we were able to detect the advertisement calls of only three frog species in the study site: *H. japonica*, *Rana dybowskii*, and *R. nigromaculata*. Based on observation of egg clutches

Table 1. Comparisons of temperature (A) and relative humidity (B) between times of calling and non-calling in three frog species. Calling activity was monitored at 10-min intervals for one day per week through the entire calling seasons of three frog species. n = number of intervals in which a given species called.

	Calling		Non-calling				
	Mean ± S.D.	n	Mean ± S.D.	n	t	*d.f.*	P
(A) Temperature (°C)							
R. dybowskii	2.95 ± 3.56	527	1.37 ± 4.71	69	−3.32	102	<0.001
R. nigromaculata	15.74 ± 2.49	502	18.04 ± 5.76	108	6.5	386	<0.001
H. japonica	19.14 ± 2.75	1434	21.17 ± 5.48	494	10.69	1685	<0.001
(B) Relative humidity (%)							
R. dybowskii	74.81 ± 23.43	527	72.56 ± 23.34	69	0.75	187	0.455
R. nigromaculata	93.78 ± 9.92	502	71.77 ± 23.26	108	−15.6	392	<0.001
H. japonica	90.74 ± 10.14	1434	76.29 ± 19.71	494	20.88	1650	<0.001

and amplectant pairs, these three frog species actually bred in the study site. Two tree frog species, *H. suweonensis* and *H. japonica*, are difficult to distinguish based on morphological characteristics. However, the advertisement call of *H. japonica* consists of only pulses, whereas that of *H. suweonensis* is composed of 4 or 5 pulses, followed by a connected pulse (S. Park, unpublished data). We did not detect the advertisement call of *H. suweonensis* at all in the acoustic monitoring data. Furthermore, previous studies based on DNA analyses (E.H. Hahm, unpublished data) and advertisement calls (S. Park, unpublished data) showed that *H. suweonensis* was not found in the study site.

In temperate environments, abiotic factors fluctuate seasonally and spatially. In anurans, temperate species are especially dependent on a combination of temperature and rainfall (Duellman and Trueb 1994; Bertoluci and Rodrigues 2002; Prado et al. 2005). The results of our year-round acoustic monitoring showed that *R. dybowskii* may be classified as a winter/spring caller. Its calling activity was brief, spanning four weeks, and intense, concentrated primarily in one week. Abiotic factors that are critical for the winter/spring callers seem to depend on species. In one survey, for example, the calling activities of the spring peeper (*Pseudacris crucifer*), the upland chorus frog (*Pseudacris feriarum*), and the southern leopard frog (*Rana sphenocephala*) were best predicted by precipitation, air temperature, and day of year, respectively (Kirlin et al. 2006). In a different survey, temperature was the most important

Table 2. Results of binary logistic regression for effects of abiotic factors on calling activity in three frog species. The binary logistic regression model included temperature, relative humidity, 24-h rainfall, and 1-day lag rainfall as predictor variables. The multivariate model was collectively significant for *R. dybowskii* (A; $\chi^2 = 78.46$, *d.f.* = 4, $P < 0.001$, $n = 596$; Nagelkerke $R^2 = 0.134$), *R. nigromaculata* (B; $\chi^2 = 129.86$, *d.f.* = 4, $P < 0.001$, $n = 610$; Nagelkerke $R^2 = 0.154$) and *H. japonica* (C; $\chi^2 = 319.23$, *d.f.* = 4, $P < 0.001$, $n = 1928$; Nagelkerke $R^2 = 0.085$). The coefficient for each predictor variable is shown below with a two-sided z that is asymptotically normal.

	Estimate	S.E.	z	P
(A) *R. dybowskii*				
Temperature	0.191	0.029	6.676	<0.001
Relative humidity	0.027	0.005	5.347	<0.001
24-h rainfall	−0.011	0.028	−0.386	0.700
1-day lag rainfall	0.078	0.013	5.999	<0.001
(B) *R. nigromaculata*				
Temperature	0.116	0.028	4.140	<0.001
Relative humidity	0.064	0.009	7.233	<0.001
24-h rainfall	−0.008	0.005	−1.753	0.080
1-day lag rainfall	−0.007	0.004	−1.514	0.130
(C) *H. japonica*				
Temperature	0.008	0.012	0.635	0.526
Relative humidity	0.051	0.005	11.306	<0.001
24-h rainfall	0.012	0.002	7.072	<0.001
1-day lag rainfall	0.002	0.001	2.018	0.044

factor for calling in *Pseudacris triseriata* and *Rana palustris*, whereas temperature, rainfall, and 1-day lag rainfall were all significant for the spring peeper (Saenz et al. 2006). In our survey, temperature, relative humidity, and 1-day lag rainfall were all critical factors for the calling activity of *R. dybowskii*.

Males of *R. dybowskii* produced advertisement calls in late winter when other frog species were not present. The calling pattern of *R. dybowskii* may represent a strategy that avoids interspecific competition at both larval and adult stages (Canelas and Bertoluci 2007). A gradual pattern of adaptation to a thermal gradient may lead to temporal partitioning of habitat in anuran communities (Richter-Boix et al. 2006). Interspecific differences in thermal physiology are associated with differences in geographic distribution and breeding phenology (John-Alder et al. 1988). We presume that thermal adaptation is markedly different between *R. dybowskii* and the two summer calling species at the study site, leading to habitat differentiation in the anuran community. Furthermore, larvae and adults of *R. dybowskii* may enjoy relatively few predators during the calling season in the study site.

The results of our acoustic monitoring indicated that *R. nigromaculata* may be a summer caller independent of weather. Two climatic factors related to rainfall were not significant for calling activity in *R. nigromaculata*. Summer callers independent of weather typically use permanent water and have relatively long breeding periods (Saenz et al. 2006). Although rice paddies are temporary wetlands, they contain water at least for the entire period of egg and larval development for *R. nigromaculata*. The calling season of *R. nigromaculata* lasted only five weeks in this study. A possible reason for such a short calling period was that the population density of this species was very low in the study site. Where the population density is high such as in coastal low-lands, the calling season is much longer, lasting for several months (Yang 2000).

The calling activity of *H. japonica* was strongly influenced by both rainfall factors. Males of *H. japonica* tended to call in rain or right after rain. Thus, this species may be a summer caller dependent on local rain. Unlike *R. nigromaculata*, which is a semiterrestrial species, *H. japonica* is classified as an arboreal species (Suzuki et al. 2007), and it typically calls out of water. In anurans, evaporative water loss is generally lower in arboreal species than in non-arboreal species (Wygoda 1984; Amey and Grigg 1995). However, *H. japonica* was the most sensitive to relative humidity, probably because it calls out of water and is relatively small in size.

Due to permeable skins, amphibians are susceptible to evaporative water loss. Terrestrial amphibians are generally nocturnal, thereby avoiding higher temperatures and lower relative humidity during the day time (Duellman and Trueb 1994). Both *R. nigromaculata* and *H. japonica* produced advertisement calls at night. However, a significant portion of calling activity in *R. dybowskii* occurred in the afternoon, and there was almost no calling activity after midnight. Evaporative water loss may not be severe under low temperatures, which would enable *R. dybowskii* to call during the daytime.

In this study we tried to understand the calling phenology and abiotic factors important for calling of anuran species in a wetland in central Korea. The long-term acoustic monitoring employed in this study is ideal for this effort. However, the duration of calling season is quite variable, depending on local weather conditions in many frog species (Wells 2007). Thus, the results of this study are preliminary; acoustic monitoring should be expanded across various habitats for each species' geographic range. Furthermore, other anuran species in central Korea are not represented in this study. Information about calling phenology and abiotic effects on calling is also necessary for conservation and restoration in amphibian species (Kim et al. 2009).

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