

Spring Voices in Korean Rice Fields: The Effect of Abiotic Variables and Syntopic Calls on the Calling Activity of the Treefrog *Dryophytes suweonensis*

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Abstract The calling activity of anurans is influenced by environmental variables and calls produced by syntopic amphibians, among other variables. Some variables have a strong influence, such as temperature and predation dilution, while others may have a periodical influence such as the moon cycle. Here, we hypothesised that the calling activity of the Suweon treefrog, *Dryophytes suweonensis*, is restricted by specific environmental variables but reinforced by the calling activity of specific syntopic anurans. Within the criteria set by the experimental design, *D. suweonensis* calling activity was significantly influenced by moon phase, temperature, date, time to sunset and the calling activity of *Pelophylax nigromaculatus* and *D. japonicus*. These variables are expected to be related to chorus size, predation, breeding phenology and competition, suggesting a broad plasticity in the calling activity of the species.

Keywords anuran, hylidae, calling activity, environmental variable, influence, Korea, North East Asia, syntopic species

1. Introduction

Anurans attract their mates through acoustic display and are prone to aggregate in choruses (Capranica, 1966; Ryan and Rand, 1998; Wilczynski and Chu, 2001), here defined as the accumulation of calling individuals at a reproductive site to attract mating partners (Bradbury, 1981; Llusia *et al.*, 2013; Höglund and Alatalo, 2014). Choruses are mainly regulated by two sets of variables. The first set includes environmental factors such as air temperature (Salvador and Carrascal, 1990; Fukuyama and Kusano, 1992), relative humidity (Oseen and Wassersug, 2002; Steelman and Dorcas, 2010), barometric pressure (Blankenhorn, 1972; Brooke *et al.*, 2002), wind speed (Oseen and Wassersug, 2002; Weir *et al.*, 2005), lunar cycle (Henzi *et al.*, 1995; Cree, 1989; Grant *et al.*, 2009), light intensity (Blair, 1961; Navas, 1996; Taylor *et al.*, 2007), and plant cover (Llusia *et al.*, 2013). However, the influence of these factors can differ between populations and species (Berg *et al.*, 2006; Llusia *et al.*, 2013).

Second, choruses are regulated by the calling activity of conspecific and syntopic species at the site (Capranica, 1966; Wells and Taigen, 1986; Ryan and Rand, 1998; Brooke *et al.*, 2002). Examples include both intraspecific effects, such as male *Hyla cinerea* waiting for the optimal timing to produce mating calls and avoid acoustic jamming (Jones *et al.*, 2014), and males regulating their calling activity based on other individuals in *Eleutherodactylus coqui* (Brush and Narins, 1989), *Dendropsophus microcephalus* (Schwartz, 1993) and *Lithobates catesbeianus* (Bates *et al.*, 2010). Examples of interspecific communication (Schwartz and Freeberg, 2008) include for example the chorus size the previous day in *Hyla* sp. (Llusia *et al.*, 2013) and eavesdropping of

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heterospecific calls by the Tungara frog (*Physalaemus pustulosus*) to detect the presence of potential predators (Phelps *et al.*, 2007). As a result, vocal behaviours in anuran breeding assemblages follow non-random structures (Bourne and York, 2001).

Because of heavy urban encroachment on natural wetlands in the Republic of Korea (Chang *et al.*, 2009) and the development of rice agriculture between 10 000 and 5000 years ago (Liu *et al.*, 2007; Fuller *et al.*, 2007, 2008), many anuran species are currently using surrogate breeding sites such as rice paddies over natural breeding grounds (Fujioka and Lane, 1997, Jang *et al.*, 2011; Borzée and Jang, 2015; Borzée *et al.*, 2017). These assemblages generally produce overlapping mating calls (Yoo and Jang, 2012) and include *Pelophylax nigromaculatus*, *P. chosenicus*, *Dryophytes japonicus* and *D. suweonensis* (Kwon *et al.*, 1991; Naito, 2012).

This project aimed at determining the influence of environmental variables and calls of syntopic anurans on the calling activity of *D. suweonensis*. We expected the calling activity of the species to be significantly influenced by the temperature and date because of the relation between these variables and physiology, chorus size and breeding phenology, while other abiotic variables were expected to have a non-significant impact. In addition, we expected a strong positive effect from the calling activity of *D. japonicus* due to predation dilution, but a negative impact from *Pelophylax nigromaculatus* due to the risk of predation.

2. Materials and Methods

2.1. Species and study sites We recorded the calling activity of *Dryophytes suweonensis* in two areas separated by at least 200 m from five independent localities and an additional independent locality (total $n = 11$) in the Paju and Gimpo areas in the Republic of Korea between 16 and 30 May 2013. The breeding activity of the species is known to be impacted by agricultural activities and the experiment was initiated only once rice paddies were flooded (Borzée *et al.*, 2018a). A total of seven species were recorded but only species calling for at least 1% of the combined data were used for the analysis. The breeding season of each of the three species retained for the analysis overlapped with the duration of the study: *D. japonicus* breeds from mid-April to mid-August (Fujioka and Lane, 1997), *D. suweonensis* breeds from early May to late June (Roh *et al.*, 2014; Borzée, 2018) and *P. nigromaculatus* breeds from May to early August (Kwon *et al.*, 1991).

2.2. Data collection Digital Flash Voice Recorders (Sony, ICD-UX523) with two stereo microphones 3 m apart were set at ground level at randomly selected sites within localities where *D. suweonensis* was known to be breeding. Recordings were initiated before 6 pm and stopped later than 8 am the consecutive day, for a night of recording per site. Leaving the recorders at the sites for a minimum of 14 h ensured the absence of observer effect and therefore provided non biased data (Bridges and Dorcas, 2000; Acevedo and Villanueva-Rivera, 2006). Because the calling activity of the species had already been temporally described (Yoo and Jang, 2012), we restricted the dataset from 6 pm to at least 4 am for subsequent analyses. When the frogs were heard calling after 4 am, we extracted the CI for 15 additional minutes after the last call of the night to ensure that we had the totality of the calling activity for each night. This resulted in a total of 5331 min of recording extracted and analysed. The selected data was listened to and annotated following the Calling Index (CI) protocol developed by the North American Amphibian Monitoring Program (Mossman *et al.* 1998; Roh *et al.*, 2014) at the precision of the minute, i.e. each minute was given a matching CI. The data was encoded for each species independently for the highest CI for each minute analysed such as: (0) absence of calling activity; (1) non-overlapping calling activity, (2) overlapping calls but individuals are countable and (3) overlapping calls with non-distinguishable individuals. In case of ambiguities for species identification, the spectrograms were analysed using the software Cool Edit 2000 (Syntrillium Software Corp.; Phoenix, USA).

Additional data were collected from the closest weather station of the National Weather Service Stations of Korea (<http://www.weather.go.kr>), for temperature and sunset time and from the National Astronomy and Space Science institute of Korea for the moon phase.

2.3. Statistical analyses The variable labelled season was defined such as day 1 being the day when both species were heard calling for the first time of the season (16 April 2013). The moon phase was measured in percent of illumination, and it was estimated to be an adequate proxy as none of the night was totally overcast. We excluded the variable locality due to the correlation with all other variables (Pearson correlation; $n = 5353$, $R > 0.46$, $P < 0.001$).

Because the dependent variable was the CI of *D. suweonensis*, an ordinal variable, we selected an Ordinal Logistic Regression for each of the CI levels to explain the impact of each variable. CI = 0 for *D. suweonensis* was set as the reference category for the analysis. The variables temperature, date, time of day, sunset time, moon phase, presence of *D. japonicus* calls and presence of *P. nigromaculatus* calls were set as covariates. The choice of the model was supported by the non-rejection of the assumptions: there were no significant outliers, the residuals

were normally distributed (visual inspection of Q-Q plot of the studentized residuals) and independent (Durbin-Watson test; DW = 0.58); predictor variables and dependent variables displayed a linear relationship and there was homoscedasticity of residuals (visualised on a plot of studentized residuals versus unstandardized predicted values). No multicollinearity was detected (collinearity statistics; VIF < 10) at the exception of the variable time to sunset (VIF = 33.70). We decided to disregard this violation of one of the assumptions for a single variable as it would not have a significant impact on the general model.

We then used the function resulting from the model to predict and confirm the average value for the variables tested resulting in CI = 3 for *D. suweonensis*. The function used was such as: Predicted CI = $b_0 + (b_1x \text{ temperature}) + (b_2x \text{ date}) + (b_3x \text{ time of day}) + (b_4x \text{ time to sunset}) + (b_5x \text{ moon phase}) + (b_6x \text{ calling activity of } Dryophytes \text{ japonicus}) + (b_7x \text{ calling activity of } Pelophylax \text{ nigromaculatus})$. All statistical analyses were conducted in SPSS 21.0 (SPSS, Inc., Chicago, IL, USA).

3. Results

In general, we found the calling index of *Dryophytes suweonensis* to be impacted by most of the variables recorded (Figure 1). The Ordinal Logistic Regression computed to explain the impact of each variable on each of the CI levels was a good fit for the

model ($P < 0.005$), explaining 59.0% of the variation (Nagelkerke test; pseudo $R^2 = 0.59$). Six variables were significant for CI = 1 and CI = 2, and only three variables were significant for CI = 3 (Table 1). The variable losing significance between CI = 1 and CI = 3 were temperature, date and time of day. While the coefficients (see B in Table 1) were consistently neutral for all CIs for date, time of day, sunset time and moon phase, they were alternatively positive and negative for the calling activity of conspecifics (Figure 1).

The highest CI for *D. suweonensis* was found to be the one at the highest temperature (19.31 °C; Table 2). All CIs have their median duration point in early June, but time of day was different between CIs, with more than 1 h difference on average between CI 1 and CI 3, and CI 3 was the one the closest to sunset time. Finally, moon phase also showed an important variation, with the peak CI closer to the new moon (illumination = 0 %) than that of the other CIs (Table 2).

The equation to confirm the predicted CI = 3 for *D. suweonensis* was such as: Predicted “CI = 3” = $652.59 + (19.31x \text{ temperature}) + (46x \text{ date}) + (199.53x \text{ time of day}) + (1.33x \text{ time to sunset}) + (14.95x \text{ moon phase}) + (1x \text{ calling activity of } D. \text{ japonicus}) + (1x \text{ calling activity of } P. \text{ nigromaculatus})$. The results of the equation (K matrix) confirmed that the variables tested for CI = 3 were indeed the best fit ($\Sigma\chi^2 = 67.39$, $P < 0.001$), such as: temperature = 19.31 °C, date = 01 June, time of day = 21:19,

Table 1 Results of the Ordinal Logistic Regression computed to explain the impact of each variable on each of the calling indices (CI) for *Dryophytes suweonensis* in its northern range in the Republic of Korea. All but one variables were significant for CI = 1 and CI = 2, while only three variables were significant for CI = 3.

		B	SE	df	P
Calling Index = 1	Temperature	0.478	0.47	1	0.013
	Date	-0.22	0.24	1	0.007
	Time of day	0.02	0.01	1	0.001
	Sunset time	-0.21	0.31	1	0.057
	Moon phase	0.06	0.03	1	< 0.001
	<i>Dryophytes japonicus</i> calls	-1.09	0.67	1	< 0.001
	<i>Pelophylax nigromaculatus</i> calls	-1.43	0.41	1	< 0.001
Calling Index = 2	Temperature	0.59	0.21	1	0.006
	Date	0.32	0.11	1	0.003
	Time of day	-0.01	0.01	1	0.001
	Sunset time	0.16	0.16	1	0.319
	Moon phase	-0.06	0.01	1	< 0.001
	<i>Dryophytes japonicus</i> calls	-0.01	0.17	1	< 0.001
	<i>Pelophylax nigromaculatus</i> calls	1.05	0.15	1	< 0.001
Calling Index = 3	Temperature	-0.48	0.48	1	0.319
	Date	0.22	0.24	1	0.375
	Time of day	-0.02	0.01	1	0.065
	Sunset time	0.02	0.3	1	0.946
	Moon phase	-0.06	0.03	1	0.044
	<i>Dryophytes japonicus</i> calls	1.09	0.67	1	0.032
	<i>Pelophylax nigromaculatus</i> calls	1.43	0.41	1	< 0.001

Table 2 Descriptive statistics for the seven variables collected describing the calling activity of *Dryophytes suweonensis* between 18:00 and 4:00 o'clock in its northern range in the Republic of Korea. Values are rounded to the closest integer (for instance day) when needed for ease of understanding. *18:00 by default as it is the earliest time for data extraction, **04:00 by default as it is the latest time for data extraction, with a 15 min delay if frogs were still calling.

		Mean	SD	Minimum	Maximum
Temperature (°C)	CI 0	16.00	2.35	13.80	24.60
	CI 1	18.39	2.43	14.00	24.50
	CI 2	18.81	1.37	15.20	21.30
	CI 3	19.31	1.06	17.40	20.30
Date (mm.dd)	CI 0	06.01	3.75	05.27	06.09
	CI 1	06.03	3.08	05.27	06.09
	CI 2	06.02	1.65	06.02	06.08
	CI 3	06.02	0.83	06.02	06.05
Time of day (hh:mm)	CI 0	00:02	02:31	18:00	04:00
	CI 1	22:37	01:51	18:06	02:39
	CI 2	22:08	01:19	19:46	01:31
	CI 3	21:19	01:12	20:11	23:24
Time to sunset (sunset time +/-s-hh:mm)	CI 0	4:12	2:55	-1:48*	8:29**
	CI 1	3:03	2:38	-1:48*	6:30
	CI 2	2:15	1:34	-0:03	7:00
	CI 3	1:33	1:21	0:22	3:35
Moon phase (%)	CI 0	60.24	35.15	1.00	100.00
	CI 1	23.82	25.00	1.00	100.00
	CI 2	14.36	6.26	4.00	41.00
	CI 3	14.36	5.23	6.00	39.00

time to sunset = time to sunset + 93 min, moon phase = 14%, and calling activity from *D. japonicus* and *P. nigromaculatus*.

4. Discussion

We had expected the calling activity of *Dryophytes suweonensis* to be significantly influenced by abiotic variables because of their relationship with physiology, chorus size and breeding phenology and this prediction was adequate. However, it should be noted that date is a confounding variable to all results presented here. Calling indices were found to increase with temperature and time of day, while a deviation from sunset time was correlated with a decrease in calling index. A plateau phase and opposite correlation would be expected for higher values for all of these three variables, although not encountered in this experiment. The variation encountered here is explained by anurans preference for calling at night in relation to predator pressure (Tuttle and Ryan, 1981). The positive increase in CI with temperature is expected to be linked to the increased mechanical properties of muscles at high temperature and therefore positively affecting male's calling rate and resulting in a higher attractiveness to females (Rome *et al.*, 1992; Prestwich, 1994; Navas and Bevier, 2001).

The moon phase was found to be negatively increasing

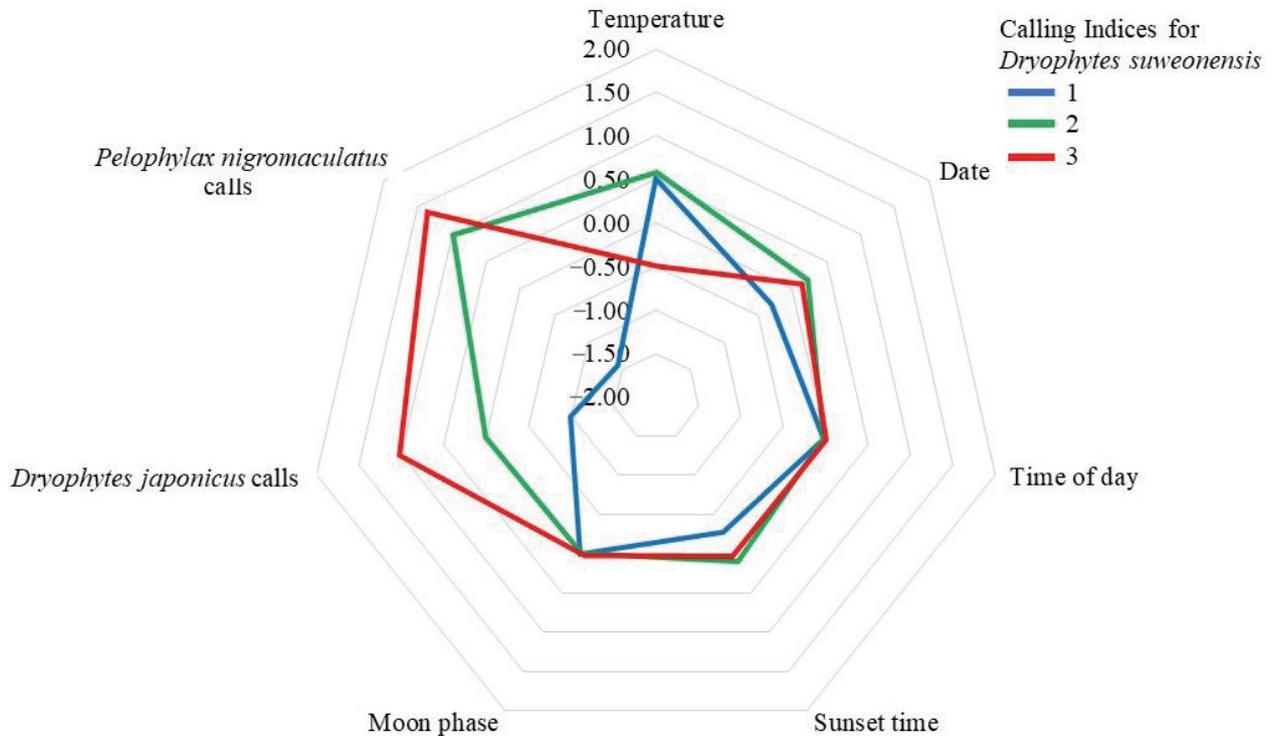


Figure 1 Importance of recorded variables on the calling activity of *Dryophytes suweonensis* in its northern range in the Republic of Korea. The variables used to create this figure are explained in Table 1.

with calling indices, a common occurrence in anurans (Grant *et al.*, 2009, reviewed by Grant *et al.*, 2012). The increase in call production during darker nights is explained by a reduction in the predation risk in comparison to full moon nights (Lima and Dill, 1990). However, calling activity may be maintained during brighter nights when light helps mate recognition (Vignoli *et al.*, 2014). This hypothesis would need to be tested for *D. suweonensis* as hybridisation is widespread between *D. suweonensis* and *D. japonicus* (Borzée and Jang, 2020). Microhabitat use by the two species is weakly segregated (Borzée *et al.*, 2016a, 2016b), and females may rely on other signals than auditory cues, such as described in *Hyla arborea* (Gomez *et al.*, 2009). In addition, factors constraining the calling activity of calling Hylids may be only partially representative of seasonal variations (Grafe and Meuche, 2005), a point also supported by the turnover in males presents at the calling site in other Hylid species (Llusia *et al.*, 2013). mating calls will initiate

Finally, we had expected a positive relation between the CI of *D. suweonensis* and the calling activity of *D. japonicus* but a negative relationship with the calling activity of *Pelophylax nigromaculatus*. Our expectations were only half correct as *D. suweonensis* displayed a positive relationship with both species, and these were the most important variables to explain the calling activity of the species (Figure 1). This overlap may be related to similar ecological requirements, but it is also expected to be linked to the lower boldness of the species (Borzée *et al.*, 2018c) and the predation dilution effect, although not demonstrated *per se* in this species. If several individuals are calling at the same time the predation risk is divided by the number of calling individuals (Hamilton, 1971; Jennions and Backwell, 1992), an effect that can involve more than two species (Martins *et al.*, 2006). The association with *P. nigromaculatus*, suggests that the dilution effect is not genus specific in *D. suweonensis* and the species is likely to be also picking on auditory signals from other anuran families. This ability to pick on cue from syntopic species may also be reinforced by the lack of spatial segregation between these species and a potential competition for acoustic space (Kim, 2015). The positive interaction present between *D. suweonensis* and the other species supports the hypothesis on chorus reinforcement developed by Wells *et al.* (1988), where a male producing mating calls will initiate a reaction in listeners through hormonal production. An example of predation dilution through eavesdropping by *D. suweonensis* is that of predation by Black-crowned night herons (*Nycticorax nycticorax*; Wolford and Boag, 1971; Yu and Hahm, 1997), a species known to be feeding on *D. suweonensis*.

In conclusion, the combination of all factors considered in this study suggests a certain plasticity in the calling activity of the species. In turn, this variability in function of environmental variables can be transformed into a calculable parameter, an

useful tool to estimate the total number of calling males during choruses (Brooke *et al.*, 2002). This can be used to determine population size when doing population size estimates for *D. suweonensis*, an endangered species (Borzée *et al.*, 2018b) for which conservation actions are urgently needed (Borzée *et al.*, 2019; Borzée and Jang, 2019). Here, all variables were significant for CI = 2 only, potentially explained by less drastic importance of variables when choruses are initiated (CI = 1), and by too few individuals to reach CI = 3 at the sites where the experiment was conducted, a likely result of the threatened status of the species (Borzée *et al.*, 2018b).

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