

Factors Affecting the Breeding Activity of the Japanese Common Toad, *Bufo japonicus formosus* (Amphibia: Bufonidae) with Special Reference to the Lunar Cycle

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Abstract: The breeding activity of the Japanese common toad, *Bufo japonicus formosus*, was monitored in Yamakita-machi, Kanagawa Prefecture and Minami-osawa, Hachioji-shi, Tokyo, during 1992–1994 and 2011–2013. The breeding activity began in late February–mid March, and lasted for one to three weeks. The number of breeding toads captured per day varied, and the effects of the lunar phase on the breeding activity were analyzed using circular statistics. Rao's spacing test indicated that large reproductive events were not uniformly distributed along the lunar cycle ($U=166.1$, $n=46$, $P<0.01$); more events occurred around the new moon and very few events occurred around the full moon. In addition, analysis of a generalized linear model incorporating both lunar phase and weather conditions, such as temperature and rainfall as predictors, indicated that the lunar phase significantly affected the breeding activity, even after taking into account the effects of weather conditions. The adaptive significance of this lunar-mediated breeding activity of the toads is discussed. Reproductive synchronization in this species may be related to the behavioral response to the lunar cycle.

Key words: *Bufo japonicus formosus*; Breeding activity; Weather conditions; Lunar cycle; Circular statistics; Reproductive synchronization

INTRODUCTION

The influence of many exogenous factors on the breeding activity of amphibians is well documented. Weather conditions such as temperature (Kusano and Fukuyama, 1989; Fukuyama and Kusano, 1992), rainfall (Kluge, 1981; Todd and Winne, 2006), wind (Robertson, 1986), or a combination of these (Blair, 1960;

Okuno, 1985; Semlitsch, 1985) are considered to be the most important factors affecting the daily fluctuation in the number of breeding adults. In addition, many other factors, including photoperiod (Both, 2008), algae odors (Savage, 1965), and predators (Woodward and Mitchell, 1990), were also reported to affect amphibian activity. Among them, the influence of the lunar cycle on some species has been suggested since the middle of the twentieth century (Church, 1960a, 1960b, 1961), but has attracted relatively little atten-

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tion. Relatively few studies have examined the possible impact of the lunar cycle on breeding and behavior. The effects of the lunar cycle have recently drawn increasing attention, and it has been suggested to be a mechanism influencing the breeding and behavior of a number of amphibian species (Deeming, 2008; Grant et al., 2009, 2013; Yetman and Ferguson, 2011; Vignoli and Luiselli, 2013).

The Japanese common toad, *Bufo japonicus formosus*, is a large and robust species that reaches sizes in excess of 100 mm snout-vent length (SVL). This species is very common in eastern Japan, from southern Hokkaido to the Kinki and San'in districts of Honshu. The toad inhabits a variety of habitats, from sea level to high mountains, and breeds explosively during early spring in still waters, such as roadside ditches, lakes, marshes, and small ponds (Maeda and Matsui, 1989). The breeding activities of *B. j. formosus* are well documented, and many aspects of its reproductive ecology, such as breeding site fidelity (Kusano et al., 1999), migration to and from the breeding sites (Hisai et al., 1987; Kusano et al., 1995), and age structure of the breeding population (Kusano et al., 2010) have been clarified. Although Aoyagi et al. (1977) and Hisai and Sugawara (1978) demonstrated that the onset of the breeding activity of this species is triggered by an increase in soil temperature, we do not yet know what factors affect the daily fluctuation of the number of breeding adults subsequent to the onset of breeding. Grant et al. (2013) reviewed the literature on amphibian responses to the lunar cycle across diverse taxa, and recommended the inclusion of the moon phase as an additional variable in predictive models of amphibian breeding or activity. The inclusion of the moon phase may produce better-fitting, more accurate models.

We conducted a census of two breeding populations of *B. j. formosus* over a three-year-period, and analyzed the relationship between the daily fluctuation of breeding activity of the toads and environmental factors, including weather variables and the lunar phase. In the present paper, we report on factors affecting

the daily fluctuations of breeding activity of *B. j. formosus*, with particular emphasis on the influence of the lunar cycle.

MATERIALS AND METHODS

Study sites

The study sites were established in Yamakita-machi, Kanagawa Prefecture and in Minami-osawa, Hachioji-shi, Tokyo. The study site in Yamakita-machi was Hannya-in temple (35°21'18"N, 139°05'42"E). The temple is located at the foot of a hilly region, at an altitude of 100 m. The study site and its surrounding area were described in detail in our previous reports (Kusano et al., 1995, 1999). Two small ponds in the temple's garden are used by *B. j. formosus* for breeding. Both ponds are 7–8 m long, 2–3 m wide, and 0.2–0.4 m deep. The linear distance between the two ponds is 30 m. Three species of frog, *Rana ornativentris*, *Glandirana rugosa*, and *Rhacophorus schlegelii*, also breed in the study ponds.

The study site in Minami-osawa was the campus of the Tokyo Metropolitan University (35°37'10"N, 139°22'56"E). There are three ponds on the campus, and at this stage, *B. j. formosus* uses only one artificial pond in front of a lecture building (No. 11) for breeding. The pond (50 m×30 m in size, 0.5 m in maximum depth, and approximately 1,300 m² in area) is located outside the northern edge of a secondary forest, consisting predominantly of *Quercus serrata*, *Q. myrsinaefolia*, and *Q. glauca*, at an altitude of 140 m within the campus. Most of the shore of the pond is open and sunny, and covered with lawn.

Monitoring of breeding activities and environmental variables

During March of 1992–1994, daily visits were made to the study ponds in Yamakita-machi to survey the breeding activity of *B. j. formosus*. Censuses were conducted at and around the two breeding ponds just after sunset (at approximately 19:00 h). Toads were captured by hand or using a dip net, measured for SVL,

weighed, and the sex was recorded. During 1992, toads were individually marked by toe clipping, whereas the toads that were first captured during the 1993–1994 monitoring were marked to denote the year of first capture by clipping a portion of the hind leg webbing. All captured toads were released immediately after these procedures were completed.

During February and March of 2011–2013, daily visits were made to the study pond in Minami-osawa. Censuses were conducted at and around the breeding pond just after sunset (at approximately 19:00 h) during 2011. During 2012–2013, we conducted a census of the breeding population just before sunset (at approximately 16:00–18:00 h), since at quiet breeding sites with little human-induced disturbance, such as the study pond, the breeding toads appear and call throughout the day, except for early morning (Hisai and Sugawara, 1978; Kusano et al., 1993). During 2011–2012, the toads captured were individually marked by passive integrated transponder (PIT) tags, and processed in the same way as was done in Yamakita-machi as described earlier. During 2013, we counted the toads captured, but they were not individually marked.

We collected lunar phase data from the National Astronomical Observatory of Japan (<http://www.nao.ac.jp/>), and meteorological variable data from the nearest weather stations of the Automated Meteorological Data Acquisition System (AMeDAS); Odawara station for Yamakita-machi and Hachioji station for Minami-osawa, which are located 10 km southeast and 8 km northwest of the respective study sites (Japan Meteorological Agency, 2014).

Statistical analysis

We used the software R 3.1.2 (R Core Team, 2014) for statistical analyses. In order to confirm whether the lunar cycle could be included as a linear factor in the following analysis, we examined the individual effect of the lunar cycle on the breeding activity as a preliminary analysis. Because the lunar phase is not a linear variable, but a circular one, the

effects of the lunar cycle should be analyzed by using circular statistics (Pewsey et al., 2013). We assigned the number of days since the new moon to each date of census as the lunar phase. These values were converted to radians by dividing by 29.5 (the length in days of the synodic lunar cycle) and then multiplying by 2π so that the data could be analyzed using circular statistics (Pewsey et al., 2013). Because the population size and census efforts differed among populations and years, data on the daily number of breeding adults captured should be adjusted for the total number of captures for each population and year, when these data are analyzed collectively. We followed the way in which Grant et al. (2009) analyzed the effects of lunar phase on the breeding activity of amphibians. We extracted the days of large reproductive events, on which the number of toads captured was >5% of the annual total number of toads captured, and examined whether the distribution of the lunar phase on the day of large reproductive events was uniform or not, using Rao's spacing test (Rao, 1976; Pewsey et al., 2013).

In addition to the lunar phase, six meteorological variables were selected as candidate factors affecting the breeding activity: the total amount of precipitation since the previous day (Rain), the rainless period (Dry), the daily maximum temperature (Tmax), the daily minimum temperature (Tmin), the daily mean wind speed (Wind), and the hours of sunshine (Sunshine) (Table 1). Because collinearity severely distorts model estimation and subsequent prediction, pairwise correlations among candidate variables were interrogated. We ascertained that all of the correlations were relatively minor; the absolute values of all correlation coefficients were less than the threshold of 0.7 (Dorman et al., 2013).

Since our preliminary analysis suggested a simple relationship between the lunar phase and the intensity of breeding activity (i.e., breeding activity was suppressed only around full moon), we could treat the lunar phase which is a circular variable as a linear variable by using the following conversion of the

variable. The lunar phase of each day was converted to the number of days from the nearest full moon as moon age (Moon in Table 1) in subsequent multivariate analysis. We analyzed the relationship between the

breeding activity and these candidate environmental variables, including population as a categorical variable, using generalized linear models with Gaussian errors and an identity link (multiple regression analysis; Fox and

TABLE 1. Candidate environmental variables affecting the breeding activities of *Bufo j. formosus*.

Variable	Unit	Abbreviation	Mean (n=132)	SD
Total amount of precipitation (48 h) since the previous day	(mm)	Rain	9.21	15.11
Rainless period	(day)	Dry	2.14	2.60
Daily maximum air temperature	(°C)	Tmax	12.20	4.07
Daily minimum air temperature	(°C)	Tmin	2.50	3.17
Daily mean wind speed	(m/sec)	Wind	2.26	1.02
Hours of sunshine	(h)	Sunshine	5.19	4.21
Moon age (the number of days to the nearest full moon)	(day)	Moon	7.69	4.35
Population	—	Pop	—	—

TABLE 2. Model selection statistics for the best 20 models of factors affecting the breeding activities. The models are ranked by AIC_c . K is the number of parameters estimated, and model probability is Akaike Weight (see Anderson, 2008).

Rank	Model i	K	logLik	AIC_c	Δ_i	Model probability w_i
1	Dry+Moon+Wind	5	-170.30	351.07	0.00	0.10
2	Dry+Moon+Sunshine+Wind	6	-170.04	352.74	1.67	0.04
3	Dry+Moon+Rain+Wind	6	-170.17	353.01	1.94	0.04
4	Dry+Moon	4	-172.36	353.03	1.95	0.04
5	Moon+Rain+Wind	5	-171.35	353.17	2.10	0.03
6	Dry+Moon+Tmax+Wind	6	-170.25	353.17	2.10	0.03
7	Dry+Moon+Tmin+Wind	6	-170.30	353.27	2.20	0.03
8	Dry+Moon+Pop+Wind	6	-170.30	353.27	2.20	0.03
9	Moon+Wind	4	-172.65	353.62	2.55	0.03
10	Dry+Moon+Rain+Sunshine+Wind	7	-169.83	354.56	3.48	0.02
11	Moon+Rain+Tmax+Wind	6	-170.96	354.60	3.53	0.02
12	Dry+Moon+Tmax	5	-172.07	354.62	3.54	0.02
13	Moon+Tmax+Wind	5	-172.10	354.69	3.61	0.02
14	Dry+Moon+Rain	5	-172.14	354.76	3.68	0.02
15	Dry+Moon+Sunshine+Tmax+Wind	7	-169.93	354.76	3.69	0.02
16	Dry+Moon+Sunshine+Tmin+Wind	7	-169.97	354.85	3.78	0.01
17	Dry+Moon+Pop+Sunshine+Wind	7	-170.04	354.97	3.90	0.01
18	Dry+Moon+Sunshine	5	-172.29	355.05	3.98	0.01
19	Dry+Moon+Rain+Tmax+Wind	7	-170.10	355.11	4.04	0.01
20	Dry+Moon+Tmin	5	-172.35	355.17	4.10	0.01

TABLE 3. Model-averaging parameter estimates of standardized partial regression coefficients. The predictors are sorted by the relative importance.

Predictor	Estimate	Unconditional SE ^a	95% Confidence Interval	Importance ^b
Moon	0.377	0.084	0.212 – 0.541	1.00
Wind	0.174	0.089	–0.001 – 0.348	0.72
Dry	0.175	0.094	–0.010 – 0.359	0.67
Rain	–0.095	0.101	–0.293 – 0.104	0.37
Tmax	0.081	0.109	–0.132 – 0.294	0.33
Sunshine	–0.045	0.130	–0.300 – 0.209	0.30
Tmin	–0.035	0.108	–0.247 – 0.177	0.27
Pop (Yamakita)	0.000	0.159	–0.312 – 0.312	0.25

^a Unconditional SE incorporates model uncertainty and thus a more conservative and appropriate uncertainty estimator for parameters (see Anderson, 2008).

^b The relative importance for a predictor is the sum of Akaike weights of the models in which the predictor was present.

Weisberg, 2011). The number of breeding adults captured for each day was treated as a response variable. All numerical variables (both response and predictors) included in the model were standardized for each year (mean=0, variance=1), because the population size and census efforts differed among populations and years.

To identify the optimal model predicting the breeding activity, we calculated the small sample-size corrected Akaike's information criterion (AIC_c) for every possible combination of the eight predictor variables, which is known as an all-subset approach (Anderson, 2008; Symonds and Moussalli, 2011). Since no single model was strongly supported by AIC_c values, we used multimodal inference. We calculated the difference (Δ_i) between the AIC_c value of the best model and the AIC_c value for each of the other models (i), and the models with $\Delta_i < 10$ were selected from the total of 256 models evaluated. We conducted a model averaging procedure using the selected models, and model averaging produced parameter and error estimates that are not conditional on any one model, but instead are derived from the weighted averages of these values across multiple models (Anderson, 2008; Symonds and Moussalli, 2011).

RESULTS

Seasonal change of breeding activity and individual effect of the lunar cycle

We monitored the breeding activities of *B. j. formosus* populations at two study sites over three consecutive years. At the Yamakita-machi site, toads began to breed from mid-March, and their breeding activities lasted for one to three weeks (Fig. 1). At the Minami-osawa site, they began breeding activities during late February to mid-March, and their breeding activities similarly lasted a few weeks (Fig. 2). At both sites, the number of male toads captured on each day was much greater than that of females (Figs. 1 and 2), and the daily number of males captured was strongly correlated with that of females captured ($r=0.743$, $df=60$, $P<0.001$ for the Yamakita-machi site; $r=0.831$, $df=68$, $P<0.001$ for the Minami-osawa site). Therefore, we only used the male census data to analyze the breeding activity of toad population in the current study. During multiple regression analysis of the factors affecting the breeding activities, we added the period of one week just before the onset of breeding to the study period of breeding activities, and thus, we analyzed data from a total number of 132 days (Table 1).

To examine the individual effect of the lunar

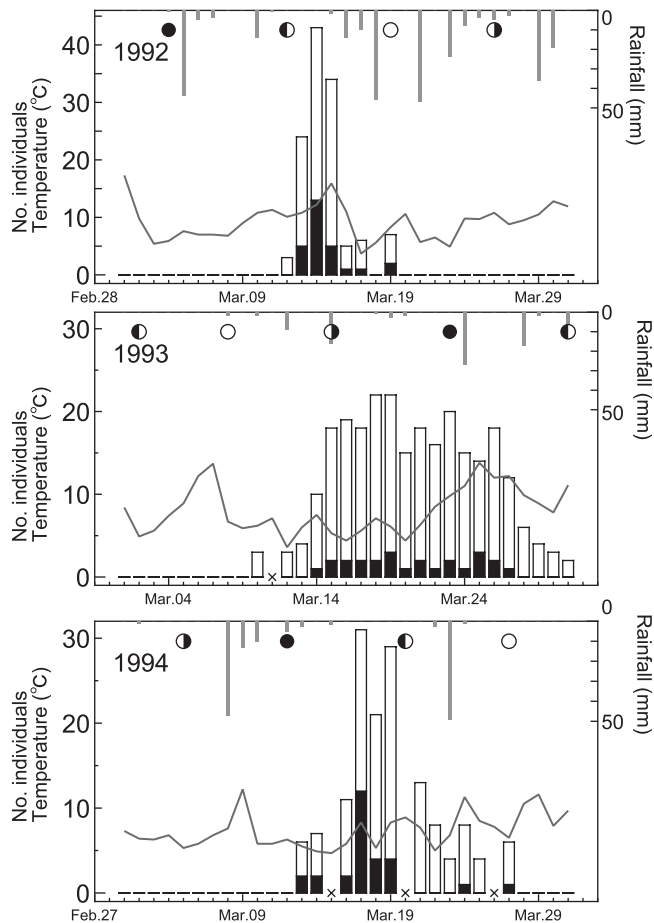


FIG. 1. Seasonal change of breeding activities of *Bufo japonicus formosus* in Yamakita-machi from 1992 to 1994. Empty and solid bars indicate the daily number of males and females captured, respectively. Meteorological conditions and lunar stage are also shown. Gray lines and narrow gray bars extending from the upper axis indicate the daily mean temperature and precipitation, respectively. Crosses in the lower axis indicate the days when we could not conduct a census.

cycle on the breeding activity, we extracted a total of 46 days as the days of large reproductive events. Rao's spacing test indicated that large reproductive events were not uniformly distributed along the lunar cycle ($U=166.1$, $n=46$, $P<0.01$). More events occurred around the new moon and very few events occurred around the full moon (Fig. 3). This confirmed that the lunar cycle can be included in the following analysis as a linear factor.

Effects of the lunar cycle and meteorological variables on the breeding activity

We analyzed the data of *B. j. formosus*

using multiple regression models incorporating meteorological variables in addition to the lunar cycle (Table 1). The global model including all eight predictor variables was significant, although the coefficient of determination was relatively small ($R^2=0.205$, $F_{8,123}=3.953$, $P<0.001$). After the evaluation of the 256 models produced by the all-subset approach based on AIC_c values, models with $\Delta_i<10$ were selected and a total of 121 models remained. The Akaike weight of the optimal model with the least AIC_c was small and the difference of AIC_c was also very small among models (Table 2); thus, model averaging was

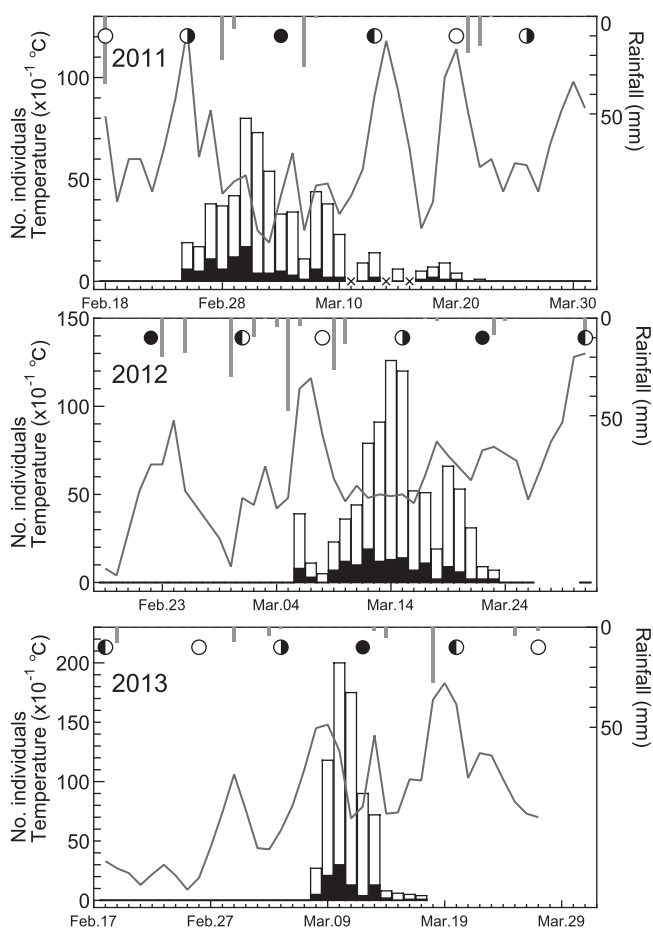


FIG. 2. Seasonal change of breeding activities of *Bufo japonicus formosus* in Minami-osawa from 2011 to 2013. Symbols are the same as in Fig. 1.

applied to this result. The relative importance of each predictor (the sum of Akaike weights of the models in which the predictor was present; Anderson, 2008) showed that Moon is included in all of the models selected and is the most important variable affecting the breeding activities among the eight candidate predictors (Table 2 and 3). In addition, Table 3 demonstrates that the 95% confidence interval of the estimate of the coefficient for Moon is from 0.212 to 0.541 and does not include zero, although those for all of the other variables include zero. This positive value of the partial regression coefficient of Moon indicates that more males were captured, when the moon phase was farther from full moon. The

multiple regression analysis including meteorological variables demonstrated a result similar to that of the analysis of the individual lunar phase effect using circular statistics. The added-variable plot (see Fox and Weisberg, 2011) of the effects of the lunar phase on the breeding activity clearly demonstrated that breeding activity became more intense when the lunar phase approached new moon, but weakened once the lunar phase approached full moon, even after taking into account the effects of the weather conditions (Fig. 4).

DISCUSSION

The effect of the lunar cycle and weather

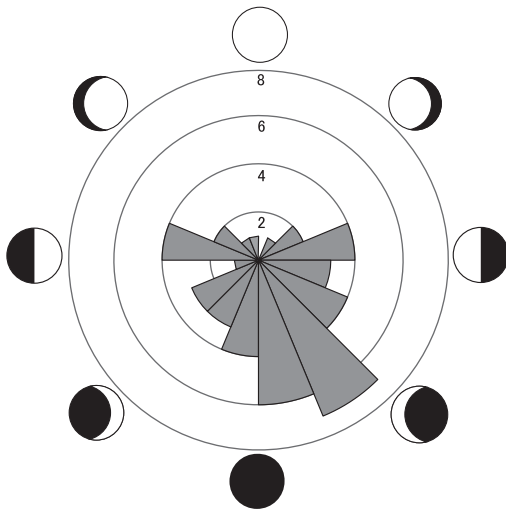


FIG. 3. Frequency of occurrence of large breeding activity events during each lunar phase at two sites over six breeding seasons. The number of males captured on each day was expressed as a percent of the total number of captures of males in each year (% captures). The days on which the above mentioned percentage exceeded 5% were selected as large reproductive events. More events occurred around the new moon and very few events occurred around the full moon (Rao's spacing test: $U = 166.1$, $n = 46$, $P < 0.01$).

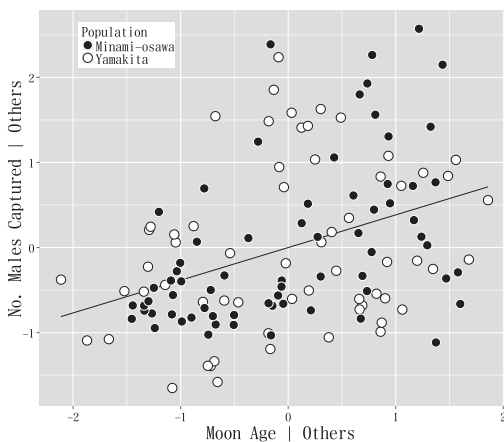


FIG. 4. Added-variable plot of the effects of lunar phase on the breeding activity of male toads. Both the moon age on the horizontal axis and the daily number of males captured on the vertical axis were adjusted for all predictors other than moon age (Table 1). A solid line shows a regression line.

variables on amphibian activity

The results of the current study clearly showed that the lunar cycle was the most important factor affecting the daily fluctuation of breeding activity after the onset of breeding, even after taking into account the effects of the weather conditions. In the current study, more breeding males appeared when the lunar phase was nearer to new moon. To the best of our knowledge, the current study may be the first report showing the lunar-mediated breeding behavior of a Japanese amphibian species.

It is well documented that many exogenous factors potentially influence the breeding activity of amphibians. The effect of the lunar phase has been recognized as one of these potential factors, but there is some contention within the scientific community regarding whether the full moon increases or decreases activity. Grant et al. (2013) reviewed the literature on amphibian responses to the lunar cycle across diverse taxa, and found that there is no significant difference between the numbers of species which increase, and those which decrease activity or reproductive behavior during a full moon.

The values of relative importance and regression coefficient suggested that wind speed and the length of the rainless period were relatively important as factors affecting the breeding activity among weather variables (Table 3). Although the magnitude of effects of these weather variables was rather small as compared with the lunar phase, the breeding activity is predicted to become higher when daily mean wind speed becomes stronger and the rainless period lasts longer. At present, we do not know the ecological significance of these effects, especially for the rainless period.

Weather variables are interrelated with each other. We examined which variables are correlated with wind speed using the AMeDAS data of Tokyo station from February to March in 2008–2013, because this station releases the data including atmospheric pressure. The results showed that correlation between daily mean wind speed and daily

mean atmospheric pressure was significant, although the correlation coefficient was not so large ($r=-0.214$, $df=353$, $P<0.001$). In early spring, when the wintry atmospheric pressure pattern breaks down in Japan, low-pressure systems which are associated with clouds and precipitation pass through the southern Kanto area (Study Group for Climate Impact and Application, 2002). Because the wind speed is negatively correlated with atmospheric pressure, high wind speed means a decrease in atmospheric pressure and thus may predict that we will have rain soon. Breeding males might not respond to wind speed itself, but to the decrease in atmospheric pressure.

The adaptive significance of lunar-mediated breeding activity

Although interesting, it is difficult to determine the reasons for varying response of amphibian species to the lunar cycle. Certain responses of amphibians are considered to be adaptive in many aspects, including predator avoidance, reproductive synchronization, visual signaling, foraging, navigation, orientation, and homing. These adaptive responses have been discussed in the context of the significance of lunar-mediated behavior. Responses to changes in prey availability, facilitation of visual signaling, and use of lunar cues in navigation and homing are considered to be less prevalent (see Grant et al., 2013), although further investigation is required. The primary reasons for changes in amphibian behavior in response to the lunar cycle appear to be predator avoidance and temporal synchronization of breeding (Grant et al., 2009, 2013; Vignoli and Luiselli, 2013).

A number of amphibian behavioral responses to the lunar cycle have been attributed to predator avoidance (Grant et al., 2009; Vignoli and Luiselli, 2013). The observed moonlight avoidance by some animal species has been related to the increased predation risk by visually oriented predators because of bright moonlight (Lima and Dill, 1990). The observed response of *B. j. formosus* to the lunar cycle may be attributed to predator

avoidance during the breeding activities. Snakes and Japanese raccoon dogs, *Nyctereutes procyonoides*, are potential predators of this toad species (Kusano et al., 1993; Wells, 2007). However, all snake species are hibernating and not active during early spring (late February–late March) when *B. j. formosus* breeds, and we found only a few toads which are considered to have been killed by the raccoon dogs for each breeding season. Thus, we think that the predation pressures are low against the breeding toads. Predator avoidance may not be important for the toads studied in the current study.

Reproductive synchronization may enhance reproductive success of breeding individuals by maximizing the pool of available breeding adults and by reducing predation risk through predator dilution/satiation not only for breeding adults themselves, but also for their offspring (Ims, 1990). In *B. j. formosus*, a large number of adults aggregate at the breeding ponds every year from the neighboring summer home ranges. Since their breeding activities lasted only for a week during some years (Figs. 1 and 2), the timing of appearance of the adults in the breeding pond may be very important for successful breeding. In this context, the lunar phase may be used as an environmental cue to adjust the timing of reproduction (Church, 1960a, 1961). A mechanism by which lunar synchrony may be controlled is described for some fish species, and is termed “lunar-mediated endogenous process” (Takemura et al., 2006). Similar endogenous processes may be the mechanisms employed to enable lunar-mediated synchronization of breeding in the case of *B. j. formosus* (Ralph, 1957), although further research is required to confirm this.

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