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Factors Affecting the Seasonal Activity of Japanese Red-Bellied Newts, *Cynops pyrrhogaster* (Amphibia: Salamandridae)

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Abstract: Seasonal activity of the Japanese red-bellied newt, *Cynops pyrrhogaster*, was monitored in Minami-ohsawa, Hachioji-shi, Tokyo, from 2016 to 2017. The number of newts in the water of a pond was counted immediately after sunset, at least once a week, except in winter. The number of newts counted varied daily, and the time-series data on newt activity were analyzed using state-space modeling to estimate the impact of weather conditions and lunar phase on the activity due to the presence of plausible temporal autocorrelation. We found that some weather conditions, such as water temperature and atmospheric pressure, had significant positive effects on newt activity. Newts became more active during nights with higher temperatures and/or higher pressure. However, we did not detect any significant effect of the lunar phase on newt activity. The most important variable affecting newt activity was water temperature. The active season of newts was estimated to be nine months from March to November. Newt activity showed a sharp decline in the nightly activity of males and an extreme female-biased sex ratio was observed in early April suggesting that the degree of nocturnality differed across seasons and the two genders. This phenomenon may be related to the presence of mating activity during this particular season.

Key words: *Cynops pyrrhogaster*; Lunar cycle; Seasonal activity; State-space model; Weather conditions

Introduction

Because amphibians are ectotherms, nearly every aspect of their physiology and behavior is affected by changing weather conditions. The influence of many exogenous factors on amphibian activity is well-documented (Wells, 2007). Breeding and non-breeding activities vary daily during the season, and these fluctuations are influenced by numerous exogenous factors, including meteorological variables, such as temperature (Kusano and Fukuyama, 1989; Fukuyama and Kusano, 1992), rainfall (Kluge, 1981; Todd and Winne, 2006), and wind (Robertson, 1986). Another variable that has recently gained considerable attention is the lunar cycle, which influences the breeding and behavior of several amphibian species

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(Deeming, 2008; Grant et al., 2009; Yetman and Ferguson, 2011; Vignoli and Luiselli, 2013). In some species, the full moon increases amphibian activity, but in others, it decreases their activity; there is no significant difference between the number of species that increase and those that decrease activity during a full moon (Grant et al., 2013). The responses to the lunar cycle cannot be generalized across taxonomic groups. Instead, they exhibit a high degree of species specificity and are directly related to the ecological characteristics of each species. Catastrophic declines in amphibian populations have been recognized globally (Houlahan et al., 2000). Population monitoring and research into factors that influence behavior (particularly when behaviors impact recruitment or mortality) are critical, and biologists are encouraged to consider the lunar phase while planning field studies (Grant et al., 2013).

The Japanese red-bellied newt, *Cynops pyrrhogaster*, is endemic to Japan and is a species of moderate size (35–70 mm in snout-vent length; Herpetological Society of Japan, 2021). It is widely distributed in Honshu, Shikoku, Kyushu, and neighboring islands. Newts inhabit a variety of habitats, from the lowlands near the seashore to the high mountains, and breed during a relatively long period from spring to early summer in still waters, such as roadside ditches, paddy fields, lakes, marshes, and small ponds; mating behaviors are also observed in autumn (Herpetological Society of Japan, 2021). This species is common in Japan, but at present, its population is at severe risk of extinction and decline, especially in the greater Tokyo area of the Kanto district (Fujita, 2018; Fukuyama and Kusano, 2023). Amphibian populations have been declining abruptly due to habitat loss and destruction caused by land development. In recent years, the aridification of breeding sites due to abandonment of paddy field cultivation, predation by exotic species, and commercial collection have become important factors causing population decline and extinction. Understanding life history and reproductive ecology is critical for the conservation of these populations. Although this newt has been recognized as a useful model research animal for over two centuries and across a broad spectrum of life science fields, our knowledge of newt populations in the field is extremely limited at present (Murakawa, 1989; Chiba et al., 2012).

We conducted a field survey of a natural population of *C. pyrrhogaster* over two consecutive years from 2016 to 2017 to monitor its seasonal and diel activities. We analyzed the relationships between newt activity and associated environmental factors, including meteorological variables and the lunar phase, using space-state modeling, since the presence of temporal autocorrelation was suspected in the ecological time series data (Auger-Méthé et al., 2021). In this study, the seasonal activity patterns, the environmental factors affecting them, sex ratio, and diel activity are reported, and subtle differences between the sexes are clarified and discussed to determine their ecological significance.

Materials and Methods

Study sites

This study was conducted over a period of two years, from February 2016 to November 2017, excluding the winter season (from December to January), in a small pond within the campus of Tokyo Metropolitan University in Minami-ohsawa, Hachioji-shi, Tokyo. The study pond ("Imori pond") was approximately 10 m in diameter and 97 m^2 in area, with a maximum depth of 0.5 m, and at an altitude of 120 m (35°37'12"N, 139°22'52"E). This pond was located in a secondary forest that consisted mainly of *Quercus serrata*, *Quercus myrsinaefolia*, and *Quercus glauca*. It served as a breeding ground for seven species of amphibians: *Hynobius tokyoensis*, *C. pyrrhogaster*, *Bufo formosus*, *Rana ornativentris*, *Glandirana reliquia*, *Zhangixalus schlegelii*, and *Zhangixalus arboreus*. To the best of our knowledge, there is no breeding site of newts within a few kilometers of the study site. Detailed descriptions of the study area have been reported by

Kusano and Inoue (2008) and Kusano et al. (2006).

Monitoring of seasonal and diel activities, sex ratio, and environmental variables

In the study pond, newts underwent overwintering between December–January, and their breeding behaviors (mating and spawning) were observed between April–June and September–November (Kusano et al., 1992). From February to November, the study pond was surveyed at least once a week, shortly after sunset (approximately 1900 h). Newt activity was monitored shortly after sunset because their activity has been reported to be predominantly nocturnal (Hayashi, 1989; Kusano, 2013). This night survey was conducted twice a week during the spawning season (April–June).

A single searcher slowly and quietly walked around the pond along the shore (39 m in length) and took approximately half an hour to count the newts in the water using an electric torch. Their positions were recorded on a map and their gender was determined based on external morphology, such as head and tail shapes (Tsutsui, 1931; Akiyama, 2020; Herpetological Society of Japan, 2021). This counting procedure was repeated three times per survey. The center portion of the pond was densely covered with *Egeria densa*, the large-flowered waterweed, resulting in the water surface being obscured more than 2 m away from the shoreline. The water level of the pond varied seasonally and the water became muddy after heavy rainfall. The areas we observed in the water were recorded on the map on each survey night, and we evaluated activity levels as the number of newts observed per unit observation area (m^2). We recorded the genders of newts observed in the water as males, females, and unknowns. The sex ratio on each survey night was calculated as a proportion of males [no. males/(no. males+no. females)].

We collected data on environmental variables, such as weather conditions, that could affect newt activity. From 2000 to 2018, including the present study period, the water temperature was monitored using a data logger placed at the bottom of the pond (approximately 15 cm below the water surface) near the shore. Relative humidity was also monitored from 2015 to 2018, using a data logger placed 1.5 m above the ground and 1 m away from the shore. Temperature and relative humidity were measured to the nearest 0.1°C and 0.1%, respectively, at intervals of 30 min. The nightly mean values were calculated from the measurements at 1800–2000 h. Illumination intensity was measured to the nearest 0.01 lux using an illumination meter (AS ONE Corporation, LM-331) at the start of the survey.

We collected lunar phase data from the National Astronomical Observatory of Japan (National Astronomical Observatory of Japan, 1994), and the lunar phase of each day was converted into the moon age, representing the number of days from the nearest full moon (see Kusano et al., 2015). Daily meteorological data on precipitation and wind were collected from the nearest weather station of the Automated Meteorological Data Acquisition System, Hachioji station, which is located 8 km northwest of the study site. Data on cloud cover and atmospheric pressure were collected from the Tokyo regional headquarters, located 34 km northeast of the study site since these data were not provided by the Hachioji station (Japan Meteorological Agency, 2022).

Newt diel activity was monitored three times in the study pond. The survey was conducted every two hours from 1600 h on November 9 to 0600 h on November 10, 1991; from 1400 h on August 8 to 1200 h on August 9, 2016; and 1800 h on November 15 to 1600 h on November 16, 2016. In the two-hour observation, a single searcher walked around the pond along the shore like the survey of seasonal activity, and counted the number of newts in the water. We did not determine the genders of newts. This counting procedure was conducted only once and not repeated unlike the survey of seasonal activity to avoid disturbing the newt activity. We used the total number of newts observed as an indicator of activity level.

Statistical analyses

Since the census data collected in the present study had a time-series aspect, the presence of temporal autocorrelation was suspected. Because the daily surveys were not conducted at the same interval, these data were converted to equally spaced time-series data for analysis. Initially, the entire daily census data were converted to weekly data by averaging the daily numbers of newts observed in each counting procedure; the weekly data were then used for all subsequent analyses. We checked the data for the magnitude of temporal autocorrelation by estimating the partial autocorrelation functions (PACFs; Venables and Ripley, 2002).

State-space models (SSMs) are important modeling frameworks for analyzing ecological time-series data. SSMs are popular because they are flexible and model natural variations in ecological processes separately from observational errors (Auger-Méthé et al., 2021). Seasonal changes in newt activity in the water were analyzed separately for years (2016 and 2017) using state-space modeling (Commandeur and Koopman, 2007; Auger-Méthé et al., 2021). To examine the differences in responses among the sex categories, SSMs were applied separately to males and females in addition to total newts. The data obtained at three counting procedures were averaged, and non-Gaussian local-level SSMs with Poisson probabilities were applied to the weekly data. To analyze the effects of environmental factors on the magnitude of seasonal activity, we incorporated these variables as explanatory variables into the local-level models (Commandeur and Koopman, 2007; Commandeur et al., 2011).

We selected eight environmental variables that could potentially affect newt activity (Table 1). Since collinearity severely distorts model estimation and subsequent prediction, pairwise correlations among the candidate variables were investigated. We ascertained that all correlations were relatively minor and the absolute values of all correlation coefficients were less than the threshold of 0.7 (Dormann et al., 2013). Environmental variables were standardized for each year (mean=0, variance=1) to promote Markov Chain Monte Carlo (MCMC) convergence and to compare the magnitude of effects among eight differently scaled explanatory variables. Weekly averaged activity levels were evaluated per unit area by incorporating the logarithms of the observation areas (m^2) as offset terms into the models.

For each sex category, the following system model was used (Baba, 2018, 2019):

$$\alpha_t = \alpha_{t-1} + \varepsilon_{1,t} \qquad \varepsilon_{1,t} \sim \mathrm{Normal}\left(0,\ \sigma_1^2\right),$$

where α_t and $\varepsilon_{1,t}$ represent the true state of activity level and disturbance, respectively, at time t. σ_1^2 is the variance of the disturbance term.

Next, we modeled the observation model as follows:

$$\lambda_t = \alpha_t + \textstyle\sum_{i=1}^{K} \beta_i x_{i,t} + \log(A_t) + r_{1,t}$$

$$r_{1,t} \sim \mathrm{Normal}\left(0,\ \sigma_{1,r}^2\right)$$

$$Y_t \sim \mathrm{Poisson}\left(e^{\lambda_t}\right),$$

where Y_t represents the number of newts observed at time t. $x_{i,t}$, and β_i represent the i th environmental variable at time t and its regression coefficient, respectively. K represents the number of environmental variables. A_t represents the pond area where newt activity was observed at time t; $r_{1,t}$, and $\sigma_{1,r}^2$ are the random effects terms and their variances, respectively. We incorporated a random effects term to consider overdispersion (Baba, 2019).

Similarly, we modeled the seasonal change in the nightly sex ratio using a non-Gaussian local-level model with binomial probability (Baba, 2018, 2019). The nightly sex ratio was evaluated as the proportion of males (males/[males+females]), and the system model used was as follows:

$$\mu_t = \mu_{t-1} + \varepsilon_{2,t} \qquad \varepsilon_{2,t} \sim \mathrm{Normal}\left(0,\ \sigma_2^2\right),$$

where μ_t and $\varepsilon_{2,t}$ represent the true state of logit-transformed nightly sex ratio (male proportion) and disturbance, respectively, at time t. σ_2^2 is the variance of the disturbance term.

Table 1. The numbers of newts observed in the night survey and environmental variables affecting the seasonal activities of newts, *Cynops pyrrhogaster*. Variables were all converted weekly mean values.

Variable	Unit	Year							
		2016				2017			
		N	Mean	SD	Range	N	Mean	SD	Range
Nightly mean water temperature at 1800–2000 h	(°C)	40	16.9	4.8	7.3–24.1	37	16.6	5.7	5.7–25.8
Daily amount of precipitation	(mm)	40	1.9	4.5	0.0–22.5	37	2.2	5.9	0.0–29.5
Nightly mean relative humidity at 1800–2000 h	(%)	40	90.2	11.9	46.6–100.0	37	86.0	11.8	61.8–100.0
Cloud cover	—	40	7.8	2.4	1.5–10.0	37	6.9	3.0	0.0–10.0
Daily mean wind speed	(m/sec)	40	2.67	0.89	1.20–4.70	37	3.02	0.98	1.60–5.60
Daily mean atomospheric pressure	(hPa)	40	1009.7	5.3	999.9–1020.0	37	1008.6	6.4	987.9–1020.2
Illumination intensity at the census time	(lux)	40	0.02	0.05	0.00–0.20	37	0.00	0.02	0.00–0.11
Moon age (the number of days to the nearest full moon)	(day)	40	7.5	4.5	0.0–14.5	37	7.4	4.3	0.5–14.5
No. males observed per counting	—	120	35.5	19.1	1–79	111	35.0	19.3	2–76
No. females observed per counting	—	120	29.5	12.7	0–62	111	28.7	13.6	0–58
No. sex unknowns observed per counting	—	120	4.0	3.6	0–13	111	3.3	3.0	0–15
Area observed	(m^2)	40	62.0	8.9	39.6–70.1	37	58.0	12.2	30.7–67.6

The observation model was as follows:

$$\text{Male}_t \sim \text{Binomial}\left(\text{Total}_t, \text{logit}^{-1}\left(\mu_t + r_{2,t}\right)\right)$$

$$r_{2,t} \sim \text{Normal}\left(0,\ \sigma_{2,r}^{2}\right),$$

where Male_t and Total_t represent the number of males observed and the combined number of both sexes at time t, respectively; and $r_{2,t}$ and $\sigma_{2,r}^2$ are the random-effects term and its variance, respectively.

All parameters were estimated using the MCMC technique in CmdStan ver. 2.30.1 via the cmdstanr package (Gabry and Češnovar, 2022) in R ver. 4.1.3 (R Core Team, 2022). The initial 2,000 MCMC samples were discarded as a warm-up; an additional 10,000 MCMC iterations were run and four chains were computed for each parameter. Convergence was confirmed by visual inspection of trace plots to ensure stationarity and mixing, and by assessing whether $\hat{R}$ values of all estimates were smaller than 1.1 (Gelman et al., 2014; Auger-Méthé et al., 2021). The posterior distributions for all parameters were summarized with the median of all MCMC samples as a point estimate and 2.5 and 97.5% of the MCMC samples as a 95% Baysian credible interval (hereafter 95% BCI).

Results

Seasonal change of newt activity

We monitored the seasonal changes in the nightly activity of newts in the pond over two consecutive years. Although only a few newts were observed before late February, newts began to appear in the water substantially in late February and were observed until November in both years. During this study, 52 and 43 surveys were conducted in 2016 and 2017, respectively, and the daily data were converted to weekly time-series data with sample sizes of 40 and 37, respectively. The number of newts of each sex category observed per counting procedure ranged from 0 to 79 (Table 1). Since the pond area where we could observe the newts varied seasonally from 30.7 to 70.1 m^2 (Table 1), the newt activity was evaluated as the number of newts observed per unit area.

PACFs were estimated using the nightly

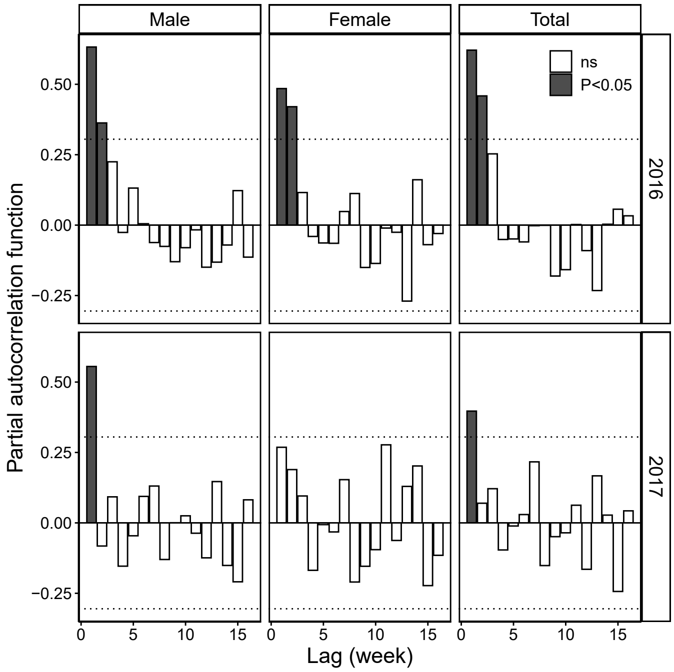

FIG. 1. Partial autocorrelation functions of the weekly averaged number of *Cynops pyrrhogaster* observed. Horizontal dotted lines depict the threshold values of significant correlation (P<0.05; $\pm 2/\sqrt{\text{sample size}}$).

mean values of three counting procedures of weekly time-series data, separately for sex categories (males, females, and the totals) and years. Significant correlations were detected for some lags (1–2) in all sex categories and years except for females in 2017 (Fig. 1), which strongly suggested that we should take account of temporal autocorrelation in the analysis of environmental variables affecting seasonal activity. We used local-level SSMs to analyze our time-series data to avoid potential problems caused by autocorrelation (Commandeur and Koopman, 2007; Auger-Méthé et al., 2021).

Seasonal changes in newt activity in the pond are shown in Fig. 2. Newt activity began in late February and increased until late March but decreased abruptly at the beginning of the spawning season in early April for males. This reduced activity was not detected in females. Thereafter, activity for total newts increased continuously and reached a peak from August to October in 2016. An abrupt decrease in activity was observed after early November. In 2017, newt activity fluctuated greatly, so it is difficult to detect a clear trend. When we look closely at Fig. 2, there is only a single estimated point (August 16 in 2017) whose 95% BCI is not overlapping with those of the neighboring points after the spawning season. The activity was unusually low on the day, although we did not know the reasons. If we look at the graph without this, gentle convex trends of the seasonal activity were similar to each year (Fig. 2).

Relationships between seasonal activity and meteorological variables and the lunar cycle

Our weekly time-series data on the number of newts observed were applied to Poisson SSMs with explanatory variables, and we estimated standardized regression coefficients for the environmental variables (Table 1, Fig. 3). Overall, the effects of water temperature,

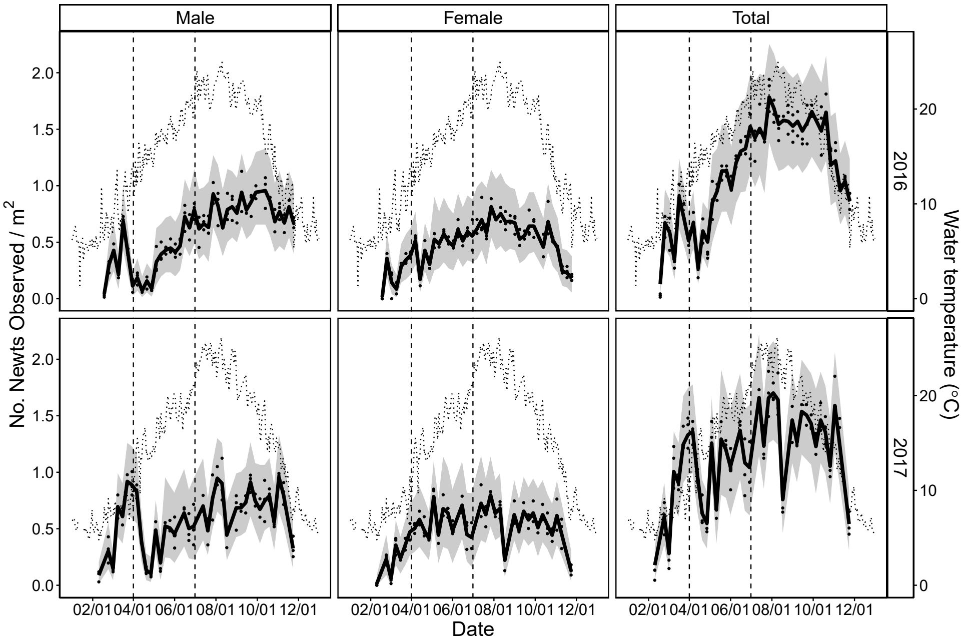

FIG. 2. Seasonal change of weekly averaged activity levels of *Cynops pyrrhogaster* from 2016 to 2017. Activity levels were evaluated as the number of newts per unit observation area. Solid lines and shaded areas depict medians and 95% Bayesian credible intervals (BCI) of the posterior distributions of activity levels predicted by state-space modelings. Small points depict the observed values (three replicates per survey), and water temperatures are depicted by dotted lines. Vertical broken lines represent the initiation and end of the spawning season of the newts.

humidity, wind speed, and atmospheric pressure were significant among the eight variables, since the 95% BCIs of the coefficients did not include zero (Fig. 3). Looking into the details, the results differed among sex categories and years. For total newts, water temperature and atmospheric pressure affected significantly in both years, but humidity did only in 2017, although the direction of the effect of humidity was the same as each year (Fig. 3). In addition, wind speed was a significant variable for total newts in 2017, but the direction of the estimated effect differed between years, although the effects of wind speed was not significant in 2016. We were unable to comprehend the reason for this highly unstable effect.

We analyzed the data separately for males and females to examine the sexual difference in the effects of environmental variables. The significant effect could be detected only in the case of water temperature for females in 2016. This may be attributed to the lack of statistical power of the test due to the insufficient sample of the nightly survey when treating both sexes separately. The magnitudes and directions of the effects of the respective variables were not so different between both sexes. We found that sexual difference was rather slight in the effects of environmental variables (Fig. 3). The coefficients estimated by the SSMs showed that the most important variable affecting newt activity was water temperature; newts were observed to be more active on warmer nights. However, we could not detect any effects of precipitation, cloud cover, illumination intensity, and moon phase on newt activity (Fig. 3).

Based on the seasonal changes in water temperature in the pond during 2000–2018, the monthly mean water temperature was observed

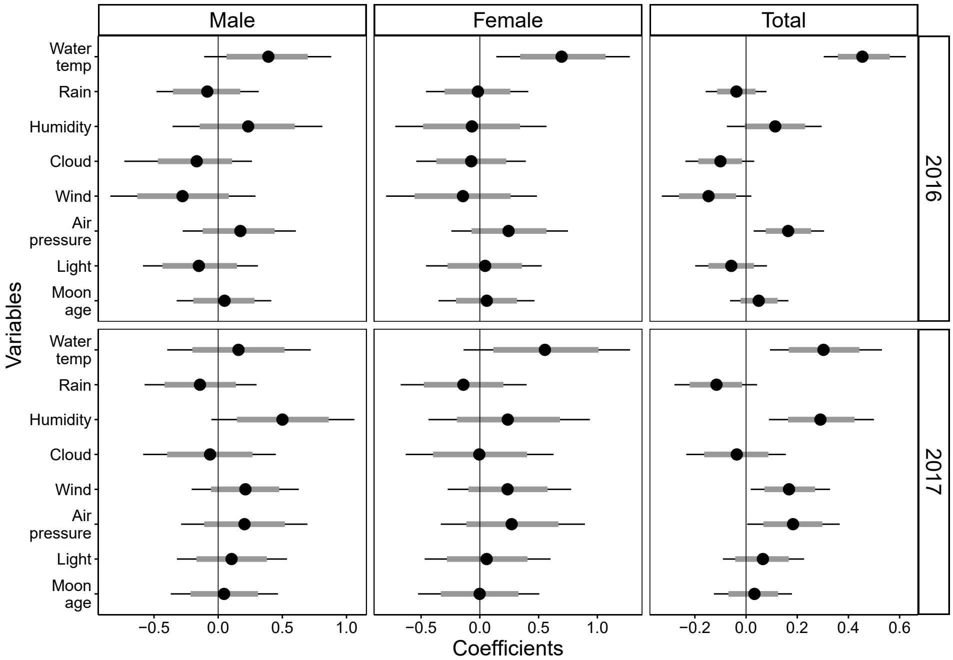

FIG. 3. Standardized regression coefficients of eight environmental variables affecting the seasonal activity of *Cynops pyrrhogaster* (Table 1). Medians and 95% BCIs of the posterior distributions of respective parameters are depicted by black circles and thin horizontal bars, respectively, 80% BCIs are represented as thick gray bars.

to be lower than 9°C from December to February. In this study, the active seasons of the newt population were nine months from March to November when monthly mean water temperature was higher than this temperature (Fig. 2).

Diel change of activity

The diel activity of the newts was surveyed thrice, and the diel changes in the total number of newts observed in the water are shown in Fig. 4. The results showed the same trend; the newts became more active during the dark hours than during the daytime. However, the degree of nocturnality varied between the surveys (November and August; Fig. 4).

Seasonal change of nightly sex ratio

The nightly sex ratios varied markedly during late February and November. The proportion of males was the highest before the spawning season (0.6–0.7) and abruptly decreased to as low as 0.25 just after the initiation of the spawning season (early April). Thereafter, the proportion of males began to increase gradually, and after the end of the spawning season, the number of males exceeded that of females (Fig. 5). The proportion of males reached 0.6–0.7 after late summer and in autumn when the newt activity in the night became the highest (Figs. 2, 5). The population sex ratio of adults in the study pond was estimated to be approximately 0.6 using a mark-recapture study employing the Cormack-Jolly-Seber model (Kusano, 2020). This suggests that the ease of detection in night surveys differs between the sexes during the spawning season. Male activity abruptly increased in late March but decreased at the beginning of the spawning season, whereas female activity increased gradually during this period (Fig. 2).

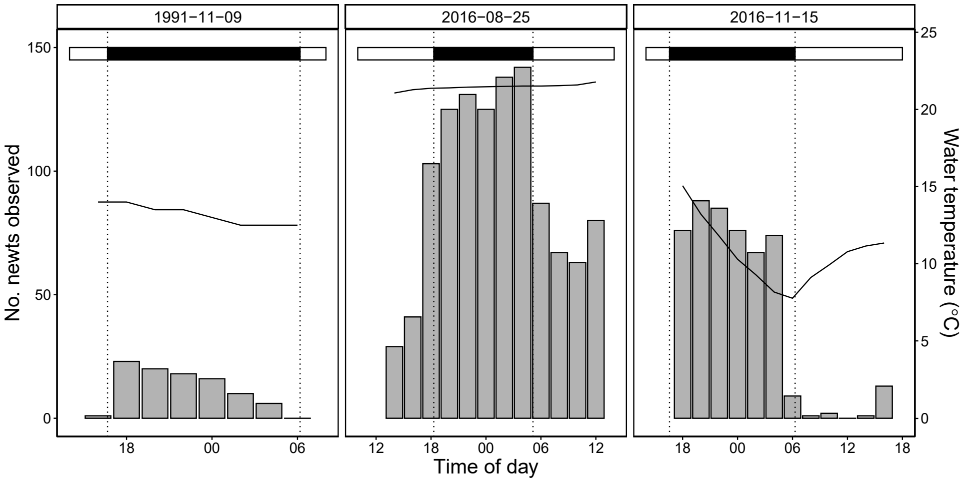

FIG. 4. Diel change of the total number of *Cynops pyrrhogaster* observed in the pond water. Solid lines show water temperatures at the time of surveys, conducted every two hours. Two vertical dotted lines represent the sunset and sunrise, respectively, and horizontal black bars represent the periods of nighttime.

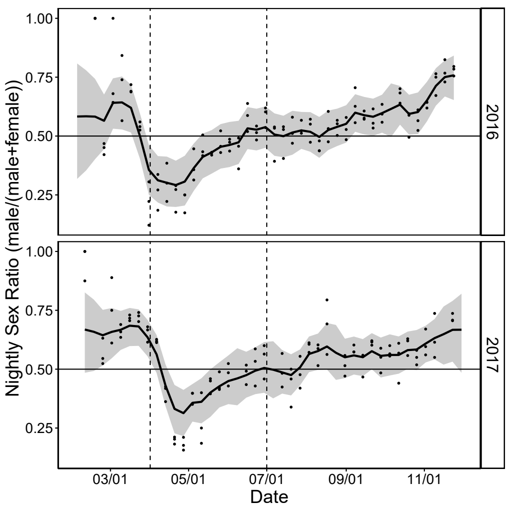

FIG. 5. Seasonal change of nightly sex ratio (proportion of males) of *Cynops pyrrhogaster* from 2016 to 2017. Solid lines and shaded areas depict medians and 95% BCI of the posterior distributions of sex ratios predicted by state-space modelings. Small points represent the observed values (three replicates per survey). Vertical broken lines represent the initiation and end of the spawning season.

DISCUSSION

Effects of meteorological factors and lunar cycle on newt activity

In the present study, newt activity was observed mainly during the nine months from March to November in the pond. To the best of our knowledge, this is the first report on the seasonal activity of this species based on quantitative field data. The seasonal trend in newt activity suggested a relatively simple convex pattern, with a flat peak in summer and early autumn. In salamanders and newts, many studies have reported that many kinds of their activities were heavily influenced by temperature, rainfall, and/or humidity (Palis, 1997; Roe and Grayson, 2008; Gravel et al., 2012; Bradley and Eason, 2021). In addition, lunar cycle also influenced activity in a few species of urodels (Hassinger and Anderson, 1970; Deeming, 2008; Grant et al., 2013). We found that some meteorological variables, such as water temperature and atmospheric pressure, had significant positive effects on newt activity; newts became more active during nights with higher temperatures and/or higher pressure. We could not detect any effects of rainfall, which might be reasonable because we observed most activity in the water.

Although the differential effects of environmental variables on amphibian activity have been reported before between the two sexes (e.g., Kusano et al., 2015, 2023), clear sexual differences in response to environmental variables were not detected in the present study. This study showed that the most important environmental variable was water temperature regardless of genders, based on standardized regression coefficients. We demonstrated that the lunar cycle did not affect seasonal changes in newt activity in the water. In the Japanese toads, *B. formosus*, inhabiting the present study site, breeding activity was affected by the lunar cycle, although it was not affected during the non-breeding season (Kusano et al., 2015, 2023). The lunar-mediated breeding activity of the toads is considered to be related to the temporal synchronization of breeding because reproductive synchronization may enhance the reproductive success of breeding individuals in explosive breeders, such as toads (Grant et al., 2009, 2013; Kusano et al., 2015). However, the breeding activity of newts lasts for several months, and most adults in the study population spend their aquatic life in the pond all year round (Kusano, 2013). Temporal synchronization may not hold significant importance, implying that the absence of lunar cycle effects may not be unusual for newts.

Sexual differences in seasonal and diel activity

The present study demonstrated sexual differences in newt activity at the beginning of the spawning season. The activity of males increased from the end of the overwintering season until late March but abruptly decreased shortly after the beginning of the spawning season (early April), whereas female activity continued to increase. This was indicated by seasonal changes in the nightly sex ratio, with a sharp decrease in the proportion of males in early April. Newt activity was positively affected by water temperature, which continued to increase during this period. However, the activity abruptly reduced only for males, and the nightly sex ratio was heavily skewed toward females. Newts reverse their active periods several times a year under semi-natural conditions (Nagai and Ohishi, 1998). In spring, mating activity increases from early morning to noon because this activity requires illumination to confirm nuptial coloration and individual discrimination (Nagai and Ohishi, 1998). As the epigamic characters of newts include color signals that play a critical role in newt sexual behavior (Himstedt, 1979), the chances of successful mating may increase if sexual behavior is conducted during those periods of the day when such signals can be best perceived by conspecifics (Griffiths, 1985). This could be the reason male newts showed diurnality in the spring (see Nagai and Ohishi, 1998), although we do not know why females did not reverse their active periods like males; the benefits of diurnality may be greater for males than for females. In summer, newts rested in the water during the morning and did not reproduce. They are mainly nocturnal during the summer (Nagai and Ohishi, 1998).

Differences in diel activity patterns between spring and summer may be explained by differences in mating activities (Nagai and Ohishi, 1998). In autumn, mating behaviors became active again in the water; however, we did not observe the clear decline in the activity of males in autumn unlike spring. Unfortunately, we do not know the reasons. Mating activity of newts are less active in autumn than in spring (Nagai and Ohishi, 1998), which may be related to the lack of decline in the activity of males in autumn. At present, we have no information on newt activity of the study population in the daytime; hence, further research on the seasonal activity of newts in the daytime is necessary to answer these questions.

Acknowledgments

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Data Availability

The Stan codes for the models generated during this study are openly available in Figshare, at 10.6084/m9.figshare.24902418.

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