Oecologia (2002) 133:616–625
DOI 10.1007/s00442-002-1067-5

BEHAVIOURAL ECOLOGY

Kerri L. Oseen · Richard J. Wassersug

Environmental factors influencing calling in sympatric anurans

Received: 27 March 2002 / Accepted: 28 August 2002 / Published online: 11 October 2002

Abstract Anuran reproduction is influenced by various biotic and abiotic factors, of which temperature and rainfall are the best studied. Here we examine the relationship between multiple abiotic environmental variables – specifically, air and water temperature, rainfall, barometric pressure, relative humidity and wind velocity – and the calling activity of five species (*Rana sylvatica*, *Pseudacris crucifer*, *Bufo americanus*, *Rana clamitans*, and *Rana catesbeiana*) in an anuran community in New Brunswick, Canada. Acoustical and environmental data were sampled hourly for 4 months during the breeding season in 1997. Logistic regression analyses indicated that each species responded to a unique combination of meteorological variables, even when calling concurrently. Calling in the spring breeding species, *R. sylvatica*, *P. crucifer*, and *B. americanus*, was most associated with the time of day (i.e., they called primarily at night), while calling in the summer breeding species, *R. clamitans* and *R. catesbeiana*, was associated primarily with high water temperature. Species with short breeding periods (i.e., explosive breeders; *R. sylvatica*, *B. americanus*) responded to fewer environmental variables than did species with prolonged breeding periods (*P. crucifer*, *R. clamitans*, *R. catesbeiana*). Prolonged breeding species responded differently to climatic variables throughout the breeding season: during the latter half of their calling periods, the time of day and a variable that predicts rain, i.e., barometric pressure, became more important, and water temperature became less important.

Keywords Anuran · Calling · Environment · Reproduction

K.L. Oseen (✉) · R.J. Wassersug
Department of Anatomy and Neurobiology, Dalhousie University, Halifax, NS B3H 1X5, Canada
e-mail: koseen@dal.ca
Fax: +1-902-4941212

Introduction

Most temperate zone anurans breed over a relatively short period of time during the spring and summer. Although anuran reproductive activity is cyclic and clearly endogenous in origin (e.g., Lofts 1974), exogenous factors also influence it. In the present study we examine how the calling activity of five sympatric anuran species varies in response to the meteorological environment during a full breeding season.

Many previous studies have found temperature and/or rainfall to be critical factors for anuran reproductive activity (e.g., Blair 1960; Heusser and Ott 1968; Heinzmann 1970). Temperate-zone species, in particular, cease migratory or reproductive activities in response to drops in temperature below species-specific thresholds. For example, woodfrogs (*Rana sylvatica*) in Michigan chorus only if air temperature exceeds 8–10°C (Howard 1980), leopard frogs (*Rana pipiens*) in Quebec spawn at a water threshold of 8°C (Gilbert et al. 1994), and European green frogs (*Rana esculenta* and *Rana ridibunda*) have calling thresholds of 12°C water temperature and 13–15°C air temperature (Obert 1975). Developmental rates and survivorship of anuran eggs and larvae are known to depend critically on temperature (Moore 1939), so it is reasonable to expect that temperature (particularly water temperature) would be one of the primary exogenous influences on reproduction (see also Navas and Bevier 2001). Other single factors, such as drops in barometric pressure (FitzGerald and Bider 1974a; Obert 1976; Bauch and Grosse 1989), light intensity (Heinzmann 1970), humidity (Bellis 1962), and wind (Henzi et al. 1995) also influence the timing of anuran reproductive activity in certain species.

Threshold levels of any environmental factor may influence anuran activity, but more than one variable likely serves as a cue for activity. Schneider (1977) found that the daily onset of calling activity in *Hyla arborea* was dependent on light intensity (≤250 lx), and that temperature did not affect calling as long as it was above a required threshold (8°C). FitzGerald and Bider (1974b) found *Bufo americanus* was more active during new moon phases compared with times of full moon, but that other weather variables, such as rain or temperature, could mask this effect. Okuno (1985) found that breeding in *Bufo japonicus* was usually correlated with warm temperatures and rainfall, but that breeding could be initiated in the absence of rain. He suggested that other biotic factors, such as calling by first-arriving males, could also stimulate calling.

Clearly, concurrent analyses of multiple variables are necessary to best predict anuran activity. Several studies have analysed anuran calling or spawning activity in the context of multiple exogenous factors (e.g., Blankenhorn 1972; Salvador and Carrascal 1990; Dorcas and Foltz 1991; Fukuyama and Kusano 1992; Henzi et al. 1995; Brooke et al. 2000). Of the abiotic variables measured to date, temperature was found to be the most common predictor of reproductive activity, followed by rain (measured concurrently or time-lagged). However, in most of those studies, variables other than temperature and rainfall were also found to be significant predictors of activity.

A problem with most previous studies was the short length of the studies and the intermittent collection of data. The present study quantitatively assesses the effects of multiple abiotic environmental factors on calling activity in a temperate anuran community on a small scale (i.e., hourly), for an entire breeding season. Specifically, we investigated whether concurrently calling species responded to the same environmental variables, and whether there were common patterns of responses among species that bred at different times of the year. We also examined whether explosive and prolonged (i.e., species with breeding periods lasting a month or longer, Wells 1977) breeding species responded to different environmental variables, and finally whether prolonged breeding species responded to the same environmental variables across their breeding season.

Materials and methods

Study site and species

This investigation was conducted at Whitetail pond in Fundy National Park, New Brunswick, Canada, from 7 May to 21 August 1997. Whitetail pond (long. 64°58'37”W, lat. 45°34'57”N) is a small, low-elevation, permanent body of water approximately 0.5 ha in size, with a mean depth of less than 1 m. Canopy cover is sparse, but the pond is entirely surrounded by mixed-wood forest, predominantly spruce and fir. A moderately used hiking path passes within 5 m of one corner of the pond.

Although early spring breeders, such as *Rana sylvatica* and *Pseudacris crucifer*, begin calling as early as late March in some parts of New Brunswick (Gorham 1970), 1997 was a late spring and the pond was not free of ice until early May. *Pseudacris crucifer* was not heard calling until several days after the start of the study, and although *R. sylvatica* was heard on the day the study began, it is assumed that due to the late spring, it was not calling for many days prior to that date.

Vocalizations of five species representing three genera of anurans were recorded during this study: American toad (*Bufo americanus*), spring peeper (*P. crucifer*), wood frog (*R. sylvatica*), green frog (*R. clamitans*), and bullfrog (*R. catesbeiana*).

Equipment

An automated recorder, which allow for periodic sampling of the acoustical environment, were used to record amphibian vocalizations in the field. The recording hardware consisted of a stereo tape recorder (Aiwa, JS-315 W), omnidirectional microphone (Radio Shack, 33–2001), and dual recycling timers (SSAC, Baldwinsville, New York). A complete description of this equipment can be found in Peterson and Dorcas (1992, 1994).

All components of the acoustical recorder except the microphone were housed inside a weather resistant plastic toolbox, and covered with a plastic awning open at each end to allow air circulation. A desiccating pack was placed inside the toolbox to prevent condensation. The microphone was covered with a 2 l plastic pop bottle with the end and one side cut off to form an awning. The awning kept rain off the microphone, while allowing sound to be recorded from all directions.

The acoustical recorder was placed approximately 1 m from the water’s edge, under vegetation. The microphone was extended out from the recorder and pointed toward the middle of the pond. Ninety-minute, normal bias, ferric oxide audiotapes were used. Calling activity for each sample period was scored as not calling (0) or calling (1) for each species. This sampling regime does not account for the number of individuals that might be calling in a given time period, and thus does not distinguish between the explosive chorus of woodfrogs and the solitary call of the bullfrog.

Air temperature (°C) and relative humidity (%) were recorded on-site using HOBO data loggers (Onset Computer Corporation, Pocasset, Mass.), and water temperature (°C) was recorded with a Vemco minilog (Vemco, Shad Bay, Nova Scotia). The water temperature data logger was placed approximately 0.5 m from shore and suspended at a depth of 20 cm. This depth was chosen because water temperature was also being recorded for another ongoing study. Air temperature and relative humidity data loggers were placed adjacent to the recorders, with their probes suspended 3 cm from the ground, and covered to prevent exposure to rain and direct sunlight.

Precipitation (mm) and wind velocity (km/h) were obtained from an Atmospheric Environmental Service (AES) of Environment Canada automated weather station located approximately 3.5 km from the pond. In addition to the relative humidity data recorded on-site, we also obtained these data from AES, because the data loggers were not in place at the site until the end of May. Relative humidity data from the two sources were well correlated (Pearson correlation coefficient r=0.6838, P=0.0001). Relative humidity obtained from the weather station was used in the analyses of early season breeding species (*R. sylvatica*, *P. crucifer*, *B. americanus*) and relative humidity measured on-site was used in the analyses of late season breeding species (*R. clamitans*, *R. catesbeiana*). Barometric pressure (kPa) was obtained from the AES meteorological station in St. John, New Brunswick, approximately 80 km away.

Sunset and sunrise times for the sampling period were obtained from the US Naval Observatory website (http://aa.usno.navy.mil/AA/data/).

Sampling protocol

Determining the appropriate length and frequency of the acoustical sampling required balancing the amount of information gained with the amount of time available for changing tapes and transcribing acoustical data. Shirose et al. (1997) found that in a 30–60 min calling survey, the majority of active anuran species in the community they studied was heard in the first 1–2 min of each hour sampled. Thus, a longer sampling time per hour does not necessarily add appreciable information. For our study, we chose a sampling regime of 1 min every hour to maximize the chances of hearing all actively calling species, while minimizing the quantity of audiotapes produced and the time spent changing tapes. Once a month between May and July, we conducted a 6 h (9 p.m. to 3 a.m.) survey at the pond, and did not hear or see any species other than those detected by the acoustical recorder.

The acoustical and AES environmental samples were all taken hourly, but not necessarily at the same time. The timer on the acoustical recorder "drifted" by a minute or so every hour, so it was not possible to get an acoustical sample every hour, exactly on the hour. The data loggers recorded the environmental parameters every 15 min. The data loggers were connected to a computer to download data, and immediately reactivated once disconnected. It was not possible to download and reactivate all the data loggers at the same time, and a sample time of every 15 min allowed for a match of the closest (within ±7.5 min) environmental recording to the acoustical recording. Environmental data from AES were recorded hourly, on the hour, and were matched to the acoustical data to the closest half hour. In this way, all data sets were merged on a single hour and day time scale.

The complete data set contained day number, time the acoustical sample was taken, calling activity for all species, and the environmental variables (taken within ±0.5 h of the acoustical sample). The data were divided into separate sets for each species, with a window of 2 weeks on either side of the "normal" calling period (Wright and Wright 1949; Gorham 1970; Gilhen 1984; Hunter et al. 1992), to ensure that the analyses incorporated ranges for the environmental variables to which each species would be exposed during its calling period.

Data sets for each of the three species with extended breeding periods (i.e., more than 1 month) were further split into two groups, approximately in the middle of the calling period, and these were designated early and late season. The *P. crucifer* data were split at day number 166 (15 June), and both the *R. catesbeiana* and *R. clamitans* data sets were separated at day number 195 (14 July).

Statistical analyses

Logistic regression was used to determine relationships between calling activity and environmental parameters (Hosmer and Lemeshow 1989). This regression model requires linearity in the relationship between the logit of the response and the independent variables, and this was determined using several approaches (Box and Tidwell 1962; Kay and Little 1986; Hosmer and Lemeshow 1989). In cases of non-linearity, a quadratic term for that environmental variable was first used. If the logit of the calling response to the quadratic term of that variable was also non-linear, a class variable was created to circumvent the non-linearity. This was done by partitioning the environmental variable into two or three groups of equal sample size, based on the number of times the animals were exposed to the variable in that range.

Hourly samples of calling activity are not independent of one another. To account for this autocorrelation in calling we used a Markov first order autoregressive model, where a lagged function, i.e., calling activity the previous hour, was added to the logistic regression (Zeger and Qaqish 1988).

A 'time of day' variable was created by classifying each acoustical sample according to when it occurred relative to sunset and sunrise: midnight to sunrise (here called 'night'), sunrise to sunset ('day'), and sunset to midnight ('evening'). This was necessary to account for the difference in the number of daylight hours each day.

We observed anurans calling immediately prior to rainfall and thought their behaviour might be in response to a drop in barometric pressure. Hence the change in barometric pressure between observations was examined in univariate and multivariate models for each species. Differences in barometric pressure were not significant variables in any statistical models, and were dropped from further analyses.

Pearson correlation coefficients among the environmental variables were determined, and where $r \geq 0.5$, one of the correlated variables was excluded from the regression analyses. In almost all cases, air and water temperature were highly correlated. For species that called from the water, air temperature was excluded from the models. Although *P. crucifer* calls primarily from the ground or bushes surrounding the pond, air temperature was excluded from this model because water temperature is a better predictor of call parameters in this species and more closely reflects body temperature (Brown and Brown 1977). If it was unknown which variable would be more biologically important to a species, we relied on the significance of the variable in a univariate model. At every step of the regression analyses, variable coefficients were examined for changing sign, and large coefficients or standard errors (Hosmer and Lemeshow 1989). No symptoms of multicollinearity were ever detected in the models.

In all cases, water temperature and time of year (i.e., week) were highly correlated. Although time of year is likely not directly detected by anurans (i.e., they are not counting the weeks), it was included as an index of the length of the calling period. The calling period for each species clearly depends on energy reserves as well as exogenous environmental factors. Calling is metabolically expensive (MacNally 1984; Pough et al. 1992), and energy reserves would be expected to decline with time (i.e., weeks), so 'time of year' or 'week' could be a credible variable as a substitute for energy reserves. However, despite the importance of the length of the calling period in this type of study, its inclusion created high standard errors for the coefficients in the regressions, and so it was excluded from the model while water temperature was retained.

The final data set for each species contained day number, time of day, calling activity (0 or 1), calling activity lagged one hour, and some form (linear, quadratic, or class) of the following variables: barometric pressure, wind velocity, precipitation, air temperature, water temperature, relative humidity. Multivariate logistic regressions were determined by backward stepwise selection, where a significance level of 0.05 was required for variables to remain in the model. All regressions were calculated using the LOGISTIC and GENMOD (generalized linear model) procedures in SAS (SAS 1996). Model fit for each regression was assessed by a non-significant ($P > 0.05$) goodness of fit test (Hosmer and Lemeshow 1989), low overall final deviance, low standard errors for the regression coefficients, and approximately uncorrelated Pearson residuals (Zeger and Qaqish 1988).

Results

Figure 1 shows the responses of all species to a single environmental variable, i.e., water temperature, which was a predictor of calling activity for most species. The results of the statistical tests incorporating all the environmental variables we measured are presented in chronological order on a species by species basis, beginning with the species that bred first. Throughout this paper, we use "response" to indicate a statistical "association" between calling and the environmental parameter.

Calling *Rana sylvatica* were recorded from 7 to 17 May. Woodfrogs called almost exclusively between sunset and sunrise (97% of calling observations; $\chi^2 = 26.6$; $P < 0.0001$; Table 1). The most significant predictor of calling in this species was calling activity in the previous hour ($\chi^2 = 48.3$; $P < 0.0001$). A logistic regression model of calling and the environmental variables when daytime observations were deleted, indicated that the only significant predictor of calling was calling in the previous hour ($\chi^2 = 37.1$; $P < 0.0001$).

Spring peepers (*Pseudacris crucifer)* called from 12 May to 15 July. This species responded differently to

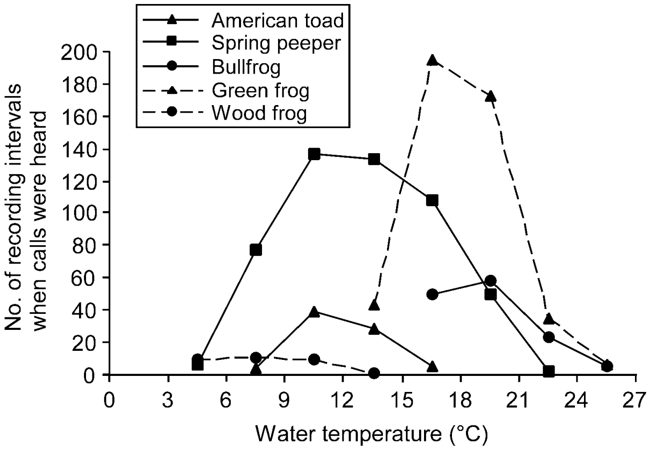


Fig. 1 The number of recording intervals in which calls were heard for the five species studied plotted against water temperature, the most common predictor of calling activity in the multivariate analyses. Each recording interval was 1 min, taken every hour during May to August, for a total of 1,938 acoustical samples. Points on the graph are data pooled over 3°C temperature intervals (e.g., 3–6°C, 6–9°C). The large area under the curve for spring peepers and green frogs reflects their extended calling season. The fewer recordings for the woodfrog and toad reflect the fact that they are explosive, short term breeders. The one species for which water temperature was not a significant variable in the logistic regression models was *Rana sylvatica*

climatic variables at the beginning and end of its breeding period. Early in the season, *P. crucifer* called primarily between sunset and sunrise ($\chi^2=225.7$; $P<0.0001$), and at low (<101 kPa; Table 1) barometric pressures ($\chi^2=4.2$; $P=0.0416$). Calling in the previous hour was also an important predictor ($\chi^2=141.1$; $P<0.0001$).

Late in the season, previous calling was the most important predictor of activity ($\chi^2=221.9$; $P<0.0001$), followed by time of day ($\chi^2=77.5$; $P<0.0001$). Water temperature ($\chi^2=11.9$; $P=0.0025$) and rain ($\chi^2=14.5$; $P=0.0001$) were also significant. During the late part of its calling season, *P. crucifer* called between sunset and midnight, at low water temperatures (≤20°C), and during rain (Table 1).

Bufo americanus was recorded calling from 24 May to 18 June. Calling activity was strongly associated with time of day (sunset to sunrise; $\chi^2=35.3$; $P<0.0001$) and mid-range water temperatures (14–18°C; Table 1; $\chi^2=15.5$; $P=0.0004$). Calling in the previous hour was the best predictor of calling ($\chi^2=121.7$; $P<0.0001$).

R. clamitans was recorded from 19 June to 8 August. Early in the season, calling of green frogs was most strongly associated with calling in the previous hour ($\chi^2=188.3$; $P<0.0001$). Other important predictors were high water temperature ($\chi^2=41.1$; $P<0.0001$), followed by time of day ($\chi^2=15.4$; $P=0.0004$), high relative humidity ($\chi^2=13.7$; $P=0.0002$) and high barometric pressure ($\chi^2=4.9$; $P=0.0257$). Green frogs called when water temperatures reached 22°C, between sunset and sunrise, when the relative humidity exceeded 90% and when the barometric pressure was >101 kPa (Table 1).

During the latter half of its calling period, *R. clamitans* responded primarily to previous calling ($\chi^2=118.6$; $P<0.0001$), time of day ($\chi^2=65.5$; $P<0.0001$), and barometric pressure ($\chi^2=5.1$; $P=0.0246$). During this period, *R. clamitans* called between sunset and sunrise, and at low barometric pressures (<101.25 kPa; Table 1).

Bullfrogs, *R. catesbeiana*, called from 18 June to 17 August. Calling early in the season was influenced most by water temperature ($\chi^2=52.3$; $P<0.0001$), and by wind ($\chi^2=9.4$; $P=0.0022$) and time of day ($\chi^2=6.0$; $P=0.0493$). This species called at high water temperatures (>20°C), low wind speeds (<15 km/h), and between sunset and sunrise (Table 1). Calling in the previous hour was also correlated ($\chi^2=20.4$; $P<0.0001$).

Late in the season, time of day ($\chi^2=27.8$; $P<0.0001$), barometric pressure ($\chi^2=21.9$; $P<0.0001$), and previous calling ($\chi^2=20.5$, $P<0.0001$) were the only significant variables. *R. catesbeiana* still called between sunset and sunrise, but primarily at low barometric pressures (≤101.25; Table 1), without the dependence on water temperature.

Discussion

Relative importance of environmental variables

Brooke et al. (2000) found that weather and chorusing by male conspecifics accounted for a small amount (approximately one-third) of the variation in calling between sites along a transect. However, they also found that while chorusing was relatively unimportant at facilitating large-scale (i.e., between sites) displays, it did influence calling on small spatial scales (within sites). The high significance of the lagged calling variable in all of our regression models (Table 1) indicates that a major predictor of calling is simply the recent calling of other conspecifics. It has also been shown that the presence of female conspecifics can influence male calling activity in some species (e.g., Henzi et al. 1995; Murphy 1999). However, in the present study we were primarily interested in how the abiotic environment influenced calling, and did not explore social facilitation further.

The two most common abiotic exogenous variables associated with calling in our study were time of day and water temperature. Many species of anurans become active shortly after sunset; e.g., *Hyla chrysoscelis* (Ritke et al. 1990), *Alytes obstetricans* (Heinzmann 1970), and *H. arborea* (Schneider 1977). MacNally (1984) found that sunset is the best predictor of call rates in *Ranidella* sp., whereas weather variables explain less of the variance. Anurans may use low ambient light as a cue for activity because there is decreased risk of attack by visually oriented, diurnal predators (e.g., birds and snakes). For all spring breeding species, time of day was the most significant predictor of call activity. *Pseudacris crucifer* was the only species to call significantly more before midnight than after. This pattern may be phylogenetic. Many ranids in temperate zones (Howard 1978; Given

Table 1 Logistic regression coefficients in the final multivariate models for each species. Significant variables are those remaining after stepwise backward elimination of non-significant variables in the final model. Where categorical variables are present in the model, the coefficients and *P*-values reflect the comparison between each level and the last level of that variable. All *P*-values were obtained via the Wald χ^2 test (SAS 1996). For all regression models in this paper: *Night* midnight–sunrise, *Day* sunrise–sunset, *Evening* sunset–midnight. A 1-h lagged calling variable was added to all models. Amount of variance explained by each species' model is approximated by the max-rescaled r^2 (Nagelkerke's pseudo-r^2; Nagelkerke 1991)

Species	Significant variables	Level	Coefficient±SE	*P*-value	Max-rescaled r^2
Rana sylvatica	Time of day	Night	–0.93±0.61	0.1301	0.5257
		Day	–3.22±0.76	<0.0001	
		Evening	–	–	
	Lagged calling		3.62±0.59	<0.0001	
Pseudacris crucifer					
Early season	Time of day	Night	–0.35±0.43	0.4246	0.7742
		Day	–3.82±0.34	<0.0001	
		Evening	–	–	
	Barometric pressure (kPa)	98.7–101	0.55±0.27	0.0436	
		>101–102.8	–	–	
	Lagged calling		3.15±0.29	<0.0001	
Late season	Time of day	Night	–1.07±0.42	0.0116	0.7548
		Day	–3.29±0.44	<0.0001	
		Evening	–	–	
	Water temperature (°C)	10–20	0.99±0.43	0.0203	
		20–22	–0.17±0.51	0.7419	
		23–29	–	–	
	Rain (mm)	0	–1.82±0.48	0.0002	
		>0	–	–	
	Lagged calling		4.23±0.36	<0.0001	
Bufo americanus	Time of day	Night	–0.34±0.36	0.3418	0.4858
		Day	–2.14±0.42	<0.0001	
		Evening	–	–	
	Water temperature (°C)	6–13	0.67±0.52	0.1953	
		14–18	1.58±0.48	0.0009	
		>19	–	–	
	Lagged calling		3.47±0.33	<0.0001	
Rana clamitans					
Early season	Water temperature (°C)	10–17	–2.08±0.34	<0.0001	0.5727
		18–21	–0.81±0.26	0.0023	
		22–29	–	–	
	Time of day	Night	–0.32±0.34	0.3636	
		Day	–1.11±0.31	0.0003	
		Evening	–	–	
	Humidity (%)	0–90	–0.90±0.25	0.0003	
		>90	–	–	
	Barometric pressure (kPa)	99–101.34	–0.48±0.22	0.0260	
		101.35–103	–	–	
	Lagged calling		2.81±0.22	<0.0001	
Late season	Time of day	Night	0.56±0.38	0.1396	0.5671
		Day	–1.73±0.32	<0.0001	
		Evening	–	–	
	Barometric pressure (kPa)	100–101.25	0.59±0.26	0.0253	
		101.26–102	–	–	
	Lagged calling		2.75±0.27	<0.0001	
Rana catesbeiana					
Early season	Water temperature (°C)	10–19	–3.90±0.77	<0.0001	0.5125
		20–29	–	–	
	Time of day	Night	–0.43±0.62	0.4840	
		Day	–1.24±0.55	0.0239	
		Evening	–	–	
	Wind (km/h)	0–15	1.36±0.47	0.0033	
		>15	–	–	
	Lagged calling		1.86±0.42	<0.0001	
Late season	Time of day	Night	0.23±0.39	0.5470	0.3375
		Day	–1.55±0.40	0.0001	
		Evening	–	–	
	Barometric pressure (kPa)	100–101.25	1.62±0.37	<0.0001	
		101.26–103	–	–	
	Lagged calling		1.6±0.35	<0.0001	

1987; Shimoyama 1989; Mohr and Dorcas 1999; Bridges and Dorcas 2000) have calling peaks after midnight, while many hylids show peaks in calling prior to midnight (Schneider 1977; Mohr and Dorcas 1999; Bridges and Dorcas 2000).

Water temperature above a certain threshold is necessary for both the adults to function and for egg and larval development of all species, although species have different physiologically preferred ranges for this variable. Spring breeding species, such as spring peepers and woodfrogs, are active early in the spring, and peepers have been heard calling at air temperatures as low as 3.5°C (Zimmitti 1999). Spring breeding species in general are physiologically adapted to cold water (see review in Salthe and Mecham 1974; John-Alder et al. 1988) and woodfrogs in particular are more adapted to cold water temperatures than any other New World anuran (Moore 1939).

It is thus not surprising that temperature was not a significant predictor of calling of woodfrogs or early season spring peepers. Woodfrogs can behaviourally mitigate the effects of cold water by spawning in shallow areas of the pond that receive more sunlight and therefore warm up more quickly (similar to the closely related and ecologically similar *Rana temporaria,* Van Gelder and Hoedemaekers 1971). Woodfrogs also oviposit in communal egg masses, which increases the temperature within the cluster relative to ambient water temperature (Howard 1980; Seale 1982; Waldman and Ryan 1983), so that embryos deep in the cluster can often survive temporary pond freezing (Moore 1939; Seale 1982). Our data suggest that toads are dependent on warmer water temperatures for calling than woodfrogs or spring peepers, even though all species breed in early spring when water temperatures are low. Toad eggs are black, which aids heat absorption, and are deposited in shallow water that warms quickly, but they are deposited in strings and do not have the added thermal advantage of communal egg masses.

The summer breeding anurans in our study, *R. clamitans* and *R. catesbeiana*, are not physiologically adapted to cold water, and high water temperature was the most significant predictor of their calling early in the season. Less dependence on temperature later in the season may indicate that a required threshold temperature has been reached. The eggs of both species are deposited as a surface film (Ryan 1978). These films do not retain heat, which may also relate to why these species are more attentive to low water temperature. Ryan (1978) found that egg masses of *R. catesbeiana* were cooler than the surrounding water temperature, and suggested that surface film egg masses mitigate the effects of high water temperatures late in the season.

Barometric pressure and relative humidity, although not as strong predictors of calling as time of day or water temperature, allow for activity with less risk of desiccation. High relative humidity may also aid in the transmission of the call, since sound travels better through humid than dry air (see Harris 1966). Only the calling of *R. clamitans* (early season), however, was sensitive to relative humidity. In the latter half of the calling period, both *R. clamitans* and *R. catesbeiana* called at low barometric pressures. Drops in barometric pressure can precede rain, possibly serving as an important cue for these animals late in the season when pond levels may be decreasing and rain is less frequent.

Although the early breeding species will breed in permanent bodies of water, such as our study pond, these species generally use temporary pools created by precipitation or snowmelt. Because of this, we expected them to respond primarily to rainfall. In fact, rainfall was not a significant variable in the regression model for any early breeding species. Rain may be an important trigger for migration to vernal ponds (*R. temporaria*, Obert 1976), but may be less important once the animals reach the pond. Church (1961) also found that while seasonal rainfall influenced the breeding period of *Bufo melanostictus* in Java, breeding activity once begun was relatively independent of rainfall. Rain may also acoustically interfere with call transmission (Dorcas and Foltz 1991) and is avoided by some calling anurans (e.g., *Bufo microscaphus*, Dorcas and Foltz 1991). Henzi et al. (1995) found that chorus attendance of male *Hyperolius marmoratus* increased following either low barometric pressure or rain, but decreased during rain itself. Fukuyama and Kusano (1992) also found a negative correlation between breeding activity in *Buergeria buergeri* and rainfall, but attributed this to flooding of the breeding site during those times. Late in the calling season, our *P. crucifer* called more during rain. The latter half of its calling period in New Brunswick extends into July and sometimes August, the hottest and driest months. During this time, activity should be more influenced by factors that decrease the risk of desiccation.

Although it would seem that all anurans should decrease activity during windy periods to avoid desiccation, the calling activity of only one of our species, *R. catesbeiana,* was significantly negatively correlated with wind (also observed by Emlen 1976). Henzi et al. (1995) found that males of *H. marmoratus* decrease chorus attendance in response to wind the previous day, presumably due to evaporative water loss. *R. catesbeiana* call from the water, so their silence during windy periods is likely due to some factor other than desiccation. Bullfrogs may cease calling during windy periods due to sound interference. The call of *R. catesbeiana* has the lowest frequency of any anuran in our study, with bimodal energy peaks at 0.2 kHz and 1.4 kHz (Capranica 1977). Wind-generated noise is greatest at such low frequencies (Bradbury and Vehrencamp 1998). As well, excess attenuation of sound occurs at frequencies lower than 1 kHz (Morton 1975), possibly exacerbating the effect of acoustical noise produced by wind.

It remains to be seen whether the patterns we observed in this study would be the same in other years. Large year-to-year variation in the environment may lead to slight differences in the calling activity of anurans each year. In particular, the influence of weather on calling of explosive breeders, such as woodfrogs and American toads, may show great year-to-year variation because they only call during a very short period of time, which may coincide with different environmental conditions. However, it seems probable that the overall importance of the meteorological variables would remain similar. Blair (1961) followed seven anuran species over 4 years in Texas. Although both the environment and the timing of calling and spawning varied between years, the response of the animals to rainfall and temperature was consistent. A recent study has demonstrated that certain anurans may be flexible in their response to different climatic conditions each year. Marsh (2000) found that the nightly correlation between breeding activity of Tungara frogs (*Physalaemus pustulosus*) and rainfall differed between wet and dry years. This species was more active on rainy nights during dry years, compared with wet years where activity did not correlate strongly with rainfall.

Spring versus summer breeders

In general, calling in spring breeding species (*R. sylvatica*, *B. americanus*, *P. crucifer*) was best predicted by time of day (i.e., sunset to sunrise), whereas calling activity of species that began breeding in the summer (*R. clamitans*, *R. catesbeiana*) was most strongly correlated with high water temperature.

Explosive versus prolonged breeders

In explosive breeders, males typically aggregate in large choruses and actively seek out females at the breeding site, whereas in prolonged breeders, males compete vocally for females, defend territories, and rarely search actively for mates (see Wells 1977). We predict that, once calling activity has begun, explosive breeders will be less responsive to their abiotic environment than prolonged breeders, because of the very short breeding period. In prolonged breeding species, females arrive at the breeding site asynchronously, and males must therefore call and maintain energy reserves over a longer period of time. Males of prolonged breeding species may be more environmentally sensitive and selective about when they call, focusing on efficiency instead of speed (Wells 1977).

In our study, prolonged breeders on average responded to more environmental variables than did explosive breeders (Table 1). For example, calling of *R. sylvatica* correlated only with time of day, whereas longer calling species, such as *R. clamitans* in the early half of its calling period, responded to the majority of the variables measured. This pattern may not be universally true, since Blankenhorn (1972) found that *Bufo calamita*, an explosive breeder, was more influenced by meteorological variables than *H. arborea*, a prolonged breeder. Similarly, Salvador and Carrascal (1990) found that meteorological variables explained less variance in species with long breeding periods; i.e., the species with longer breeding periods were less dependent on environmental variables. However, all species that they studied had prolonged breeding periods, ranging in length from 1 to 2 months.

Prolonged breeders: early versus late season calling

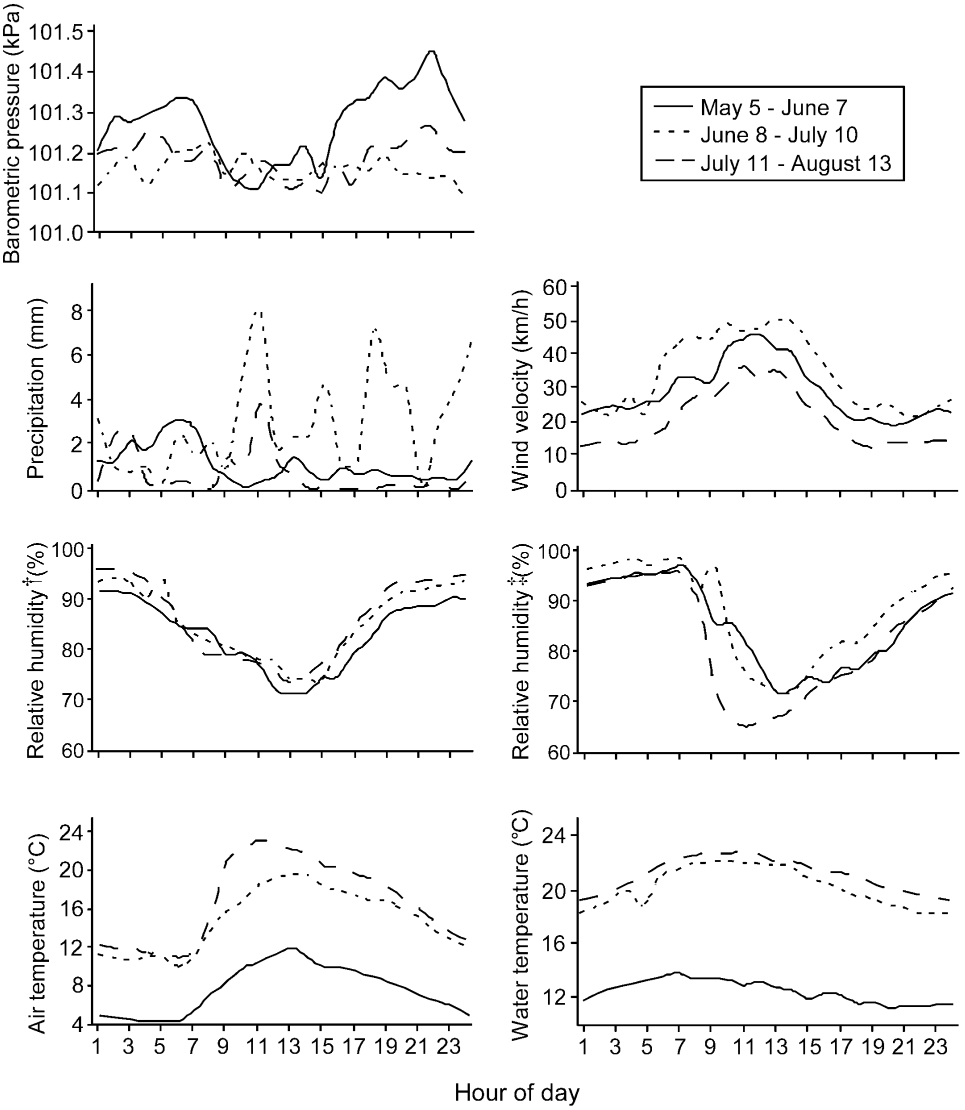
The association between calling and the climatic variables we measured differed between early and late season for the three prolonged breeding species in our study (Table 1). It should be noted that the patterns of variance in certain environmental variables, i.e., barometric pressure and precipitation, also differed over the season (Fig. 2). For example, when these two environmental variables had the highest variance during the season, they were also significant predictors of *P. crucifer* calling. Barometric pressure was a significant predictor of activity in the *P. crucifer* early season model, and this variable had the highest variance early in the season. Later, when rainfall became more variable, it also became a stronger predictor of activity for *P. crucifer*. *P. crucifer* responded to more meteorological variables in the latter part of their calling period in comparison with the early season, indicating that they may be slightly more selective about when to call later in the breeding period.

It is easiest to extract common patterns in the response of prolonged breeding species to the environment from the two species that have similar reproductive strategies, *R. catesbeiana* and *R. clamitans* (Wells 1976; Howard 1978). Both species had similar responses to the environment in the early and late portions of their breeding seasons. The change in their response to the environment over the season may be due to a change in the composition of the breeding population. Later spawning events may consist of older females that have already mated that season, and late-arriving females that have not yet mated. In any case, it seems likely that fewer females will be arriving at the breeding site as the season progresses. If males are more selective about calling late in the season when their chances of mating are low, they may conserve energy and enhance lifetime reproductive success (Runkle et al. 1994).

We found that males of both *R. catesbeiana* and *R. clamitans* responded to fewer variables later in the season, and the major abiotic predictor of calling shifted from water temperature to time of day (Table 1). Howard (1978) found that the location of bullfrog choruses throughout the summer varies according to water temperature. Early season choruses form in the regions of highest water temperature, and successive choruses move to progressively cooler areas, possibly to avoid extreme water temperatures. A certain water temperature threshold may be necessary, but if achieved early in the breeding season, becomes less important later in the season.

Clinal variation in meteorological factors can result in differences in species' responses along their geographical range, as suggested for *Bufo viridis* (Jørgensen 1992). Although woodfrogs could possibly use different environmental cues during reproduction in various parts of

Fig. 2 Hourly averages of environmental variables measured at three periods during the season. Each hour represents an average of that variable at that hour across all days in that sample period. This graph shows both hourly and seasonal variation in the environmental variables. Although there is great hourly variation, the overall pattern of variance in most environmental parameters is similar at different periods in the season. The exceptions are rain, which is more variable in the middle of the season, and barometric pressure, which is more variable early in the season. (†Recorded at the AES weather station. ‡Recorded on-site)



their range, the air and water temperature thresholds appear to be similar throughout their range (e.g., Herreid and Kinney 1967; Meeks and Nagel 1973). In our study, calling in *R. clamitans* and *R. catesbeiana* is associated with water temperature only in the early breeding period, but a similar pattern might not be observed in southerly portions of their geographical ranges. In southern regions, warm water may be available at the beginning of the breeding period, making the animals less selective about water temperature at that time. Early in the breeding period populations located further south may show a similar response to environmental variables as northern populations do later in the breeding period.

It is also possible that a shift in the environmental preferences of anurans later in the season may reflect a change in their reasons for calling. It has recently been shown that calling by male midwife toads (*Alytes muletensis*) stimulates females to mature eggs (Lea et al. 2001). It may similarly turn out that late season vocalizations by other anurans influences female frogs in a way that positively affects their egg production and breeding success the following year. Pope (1964) suggests that late season calling may be associated with sperm production, and in *R. temporaria*, spermatogenesis begins shortly after spawning ceases, in readiness for the following spring (Lofts 1974). It is also possible that late season calling affects newly metamorphosed individuals, helping them gain familiarity with their natal ponds.

Based on our data, some generalizations can be made about the response of an anuran community to abiotic environmental factors: (1) each species in an anuran community may respond to different combinations of environmental variables, (2) spring and summer breeding species can respond to different primary environmental cues during reproduction, (3) explosive breeding species respond to fewer environmental variables than do prolonged breeding species, and (4) prolonged breeding species may change their response to the environment over the course of the breeding season.

Acknowledgements We thank M. Leonard, C. Staicer, C. Peterson, J. Caldwell, K. Wells and A.S. Rand for many helpful comments on earlier drafts of this manuscript. We thank W. Blanchard and M. Mazerolle for statistical advice and D. Clay for initiating this project. M. Dorcas provided the automated acoustical recorder, M. Fejtek and S. Gerriets provided technical assistance and J. Blair assisted with data collection. This research was supported by Parks Canada, the Environmental Monitoring and Assessment Network of Canada, a Patrick Lett graduate scholarship (K.L.O.), and the Natural Sciences and Engineering Research Council of Canada (R.J.W.).

References

Bauch S, Grosse W-R (1989) Der Nachweis einer Nachlaichzeit beim Laubfrosch, *Hyla a. arborea* (L.) (Amphibia, Anura, Hylidae). Hercynia 26:425–429

Bellis ED (1962) The influence of humidity on woodfrog activity. Am Midl Nat 68:139–148

Blair WF (1960) A breeding population of the Mexican toad (*Bufo valliceps*) in relation to its environment. Ecology 41:165–174

Blair WF (1961) Calling and spawning seasons in a mixed population of anurans. Ecology 42:99–110

Blankenhorn HJ (1972) Meteorological variables affecting onset and duration of calling in *Hyla arborea* L. and *Bufo calamita calamita* Laur. Oecologia 9:223–234

Box GEP, Tidwell PW (1962) Transformation of the independent variables. Technometrics 4:531–550

Bradbury JW, Vehrencamp SL (1998) Principles of animal communication. Sinauer, Sunderland, Mass.

Bridges AS, Dorcas ME (2000) Temporal variation in anuran calling behavior: implications for surveys and monitoring programs. Copeia 2000:587–592

Brooke PN, Alford RA, Schwarzkopf L (2000) Environmental and social factors influence chorusing behaviour in a tropical frog: examining various temporal and spatial scales. Behav Ecol Sociobiol 49:79–87

Brown LE, Brown JR (1977) Comparison of environmental and body temperatures as predictors of mating call parameters of spring peepers. Am Midl Nat 97:209–211

Capranica RR (1977) Auditory processing of vocal signals in anurans. In: Taylor DH, Guttman SI (eds) The reproductive biology of amphibians. Plenum Press, New York, pp 337–355

Church G (1961) Seasonal and lunar variation in the numbers of mating toads in Bandung (Java). Herpetologica 17:122–126

Dorcas ME, Foltz KD (1991) Environmental effects on anuran advertisement calling. Am Zool 31:111A

Emlen ST (1976) Lek organization and mating strategies in the bullfrog. Behav Ecol Sociobiol 1:283–313

FitzGerald GJ, Bider JR (1974a) Seasonal activity of the toad *Bufo americanus* in southern Quebec as revealed by a sand-transect technique. Can J Zool 52:1–5

FitzGerald GJ, Bider JR (1974b) Influence of moon phase and weather factors on locomotory activity in *Bufo americanus*. Oikos 25:338–340

Fukuyama K, Kusano T (1992) Factors affecting breeding activity in a stream-breeding frog, *Buergeria buergeri*. J Herpetol 26:88–91

Gilbert M, Leclair R Jr, Fortin R (1994) Reproduction of the northern leopard frog (*Rana pipiens*) in floodplain habitat in the Richelieu river, P. Quebec, Canada. J Herpetol 28:465–470

Gilhen J (1984) Amphibians and reptiles of Nova Scotia. Nova Scotia Museum, Halifax, Nova Scotia

Given MF (1987) Vocalization and acoustic interactions of the carpenter frog, *Rana virgatipes*. Herpetologica 43:467–481

Gorham SW (1970) The amphibians and reptiles of New Brunswick. Monographic Series No. 6. New Brunswick Museum, Saint John, New Brunswick

Harris CM (1966) Absorption of sound in air versus humidity and temperature. J Acoust Soc Am 40:148–159

Heinzmann U (1970) Untersuchungen zur bio-akustik und ökologie der geburtshelferkröte, *Alytes o. obstetricans* (Laur.). Oecologia 5:19–55

Henzi SP, Dyson ML, Piper SE, Passmore NE, Bishop P (1995) Chorus attendance by male and female painted reed frogs (*Hyperolius marmoratus*): environmental factors and selection pressures. Funct Ecol 9:485–491

Herreid CF, Kinney S (1967) Temperature and development of the wood frog, *Rana sylvatica*, in Alaska. Ecology 48:579–590

Heusser H, Ott J (1968) Wandertrieb und populationsspezifische Sollzeit der Laichwanderung bei der Erdkröte, *Bufo bufo* (L.). Rev Suisse Zool 75:1005–1022

Hosmer DW Jr, Lemeshow S (1989) Applied logistic regression. Wiley, New York

Howard RD (1978) The evolution of mating strategies in bullfrogs, *Rana catesbeiana*. Evolution 32:850–871

Howard RD (1980) Mating behavior and mating success in wood frogs, *Rana sylvatica*. Anim Behav 28:705–716

Hunter ML, Albright J, Arbuckle J (1992) The amphibians and reptiles of Maine. Maine Agric Exp Stn Bull 838

John-Alder HB, Morin PJ, Lawler S (1988) Thermal physiology, phenology and distribution of tree frogs. Am Nat 132:506–520

Jørgensen CB (1992) Growth and reproduction. In: Feder ME, Burggren WW (eds) Environmental physiology of the amphibians. University of Chicago Press, Chicago, pp 439–466

Kay R, Little S (1986) Assessing the fit of the logistic model: a case study of children with haemolytic uraemic syndrome. Appl Stat 35:16–30

Lea J, Dyson M, Halliday T (2001) Calling by male midwife toads stimulates females to continue maturing their eggs. Anim Behav 61:373–377

Lofts B (1974) Reproduction. In: Lofts B (ed) Physiology of the amphibia, vol II. Academic Press, New York, pp 107–218

MacNally RC (1984) On the reproductive energetics of chorusing males: costs and patterns of call production in two sympatric species of *Ranidella* (Anura). Oikos 42:82–91

Marsh DM (2000) Variable responses to rainfall by breeding Tungara frogs. Copeia 2000:1104–1108

Meeks DE, Nagel JW (1973) Reproduction and development of the woodfrog, *Rana sylvatica* in eastern Tennessee. Herpetologica 29:188–191

Mohr JR, Dorcas ME (1999) A comparison of anuran calling patterns at two Carolina bays in South Carolina. J Elisha Mitchell Sci Soc 115:63–70

Moore JA (1939) Temperature tolerance and rates of development in the eggs of Amphibia. Ecology 20:459–478

Morton ES (1975) Ecological sources of selection on avian sounds. Am Nat 109:17–34

Murphy CG (1999) Nightly timing of chorusing by male barking treefrogs (*Hyla gratiosa*): the influence of female arrival and energy. Copeia 1999:333–347

Nagelkerke NJD (1991) A note on a general definition of the coefficient of determination. Biometrika 78:691–692

Navas CA, Bevier CR (2001) Thermal dependency of calling performance in the eurythermic frog *Colostethus subpunctatus*. Herpetologica 57:384–395

Obert H-J (1975) The dependence of calling activity in *Rana esculenta* Linné 1758 and *Rana ridibunda* Pallas 1771 upon exogenous factors (Ranidae, Anura). Oecologia 18:317–328

Obert H-J (1976) Some effects of external factors upon the reproductive behavior of the grass frog *Rana t. temporaria* L. (Ranidae, Anura). Oecologia 24:43–55

Okuno R (1985) Studies on the natural history of the Japanese toad, *Bufo japonicus japonicus*. VIII. Climatic factors influencing the breeding activity. Jpn J Ecol 35:527–535

Peterson CR, Dorcas ME (1992) The use of automated data-acquisition techniques in monitoring amphibian and reptile populations. In: McCullough DR, Barrett RH (eds) Wildlife 2001: populations. Elsevier, Essex, pp 369–378

Peterson CR, Dorcas ME (1994) Automated data acquisition. In: Heyer WR, Donnelly MA, McDiarmid RW, Hayek L-AC, Foster MS (eds) Measuring and monitoring biological diversity.

Standard methods for amphibians. Smithsonian Institution, Washington, pp 47–57

Pope CH (1964) Amphibians and reptiles of the Chicago area. Chicago Natural History Museum, Chicago

Pough FH, Magnusson WE, Ryan MJ, Wells KD (1992) Behavioral energetics. In: Feder ME, Burggren WW (eds) Environmental physiology of the amphibians. University of Chicago Press, Chicago, pp 395–436

Ritke ME, Babb JG, Ritke MK (1990) Life history of the gray treefrog (*Hyla chrysoscelis*) in Western Tennessee. J Herpetol 24:135–141

Runkle LS, Wells KD, Robb CC, Lance SL (1994) Individual, nightly, and seasonal variation in calling behavior of the gray tree frog, *Hyla versicolor*: implications for energy expenditure. Behav Ecol 5:318–325

Ryan MJ (1978) A thermal property of the *Rana catesbeiana* (Amphibia, Anura, Ranidae) egg mass. J Herpetol 12:247–248

Salthe SN, Mecham JS (1974) Reproductive and courtship patterns. In: Lofts B (ed) Physiology of the amphibia, vol II. Academic Press, New York, pp 310–521

Salvador A, Carrascal LM (1990) Reproductive phenology and temporal patterns of mate access in Mediterranean anurans. J Herpetol 24:438–441

SAS (1996) SAS STAT user's guide release 6.12. SAS Institute, Cary, N.C.

Schneider H (1977) Acoustic behavior and physiology of vocalization in the European tree frog, *Hyla arborea* (L.). In: Taylor DH, Guttman SI (eds) The reproductive biology of amphibians. Plenum Press, New York, pp 295–335

Seale DB (1982) Physical factors influencing oviposition by the woodfrog, *Rana sylvatica*, in Pennsylvania. Copeia 1982:627–635

Shimoyama R (1989) Breeding ecology of a Japanese frog, *Rana porosa*. In: Matsui M, Hikada T, Goris RC (eds) Current herpetology in East Asia. Herpetological Society of Japan, Kyoto, pp 323–331

Shirose LJ, Bishop CA, Green DM, MacDonald CJ, Brooks RJ, Helferty NJ (1997) Validation tests of an amphibian call count survey technique in Ontario, Canada. Herpetologica 53:312–320

Van Gelder JJ, Hoedemaekers HCM (1971) Sound activity and migration during the breeding period of *Rana temporaria* L. *R. arvalis* Nilsson, *Pelobates fuscus* Laur. and *Rana esculenta* L. J Anim Ecol 40:559–568

Waldman B, Ryan MJ (1983) Thermal advantage of communal egg mass deposition in wood frogs (*Rana sylvatica*). J Herpetol 17:70–72

Wells KD (1976) Multiple egg clutches in the green frog (*Rana clamitans*). Herpetologica 32:85–87

Wells KD (1977) The social behavior of anuran amphibians. Anim Behav 25:666–693

Wright AH, Wright AA (1949) Handbook of frogs and toads of the United States and Canada, 3rd edn. Comstock, Cornell University Press, Ithaca, N.Y.

Zeger SL, Qaqish B (1988) Markov regression models for time series: a quasi-likelihood approach. Biometrics 44:1019–1031

Zimmitti S (1999) Individual variation in morphological, physiological, and biochemical features associated with calling in spring peepers (*Pseudacris crucifer*). Physiol Biochem Zool 72:666–676