Journal of Natural History
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713192031

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Online publication date: 02 December 2009

To cite this Article Canavero, Andrés and Arim, Matías(2009) 'Clues supporting photoperiod as the main determinant of seasonal variation in amphibian activity', Journal of Natural History, 43: 47, 2975 — 2984
To link to this Article: DOI: 10.1080/00222930903377539
URL: http://dx.doi.org/10.1080/00222930903377539

Journal of Natural History
Vol. 43, Nos. 45–48, December 2009, 2975–2984

Clues supporting photoperiod as the main determinant of seasonal variation in amphibian activity

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(Received 21 January 2009; final version received 30 September 2009)

Organism survival and reproduction are affected by the ability to synchronize behaviour and physiological condition to the season, typically using photoperiod. However, temperature and rainfall have been repeatedly invoked as determinants of annual reproductive cycles in amphibians. This putative role of environmental conditions determining amphibians' activity was recently challenged in favour of photoperiod or a combination of environmental variables as more plausible clues. We evaluated the alternative variables potentially used by amphibians to track season fluctuations. The seasonality of a system was captured in a structural equation model, which identified photoperiod as the variable that represents seasonal variations in amphibian richness and climatic conditions. Congruently, reconstruction of amphibian seasonality with a sinusoidal model captured the same information as a linear regression between richness and photoperiod. Available evidence suggests that amphibians could be tracking photoperiod, over temperature and rainfall, as the proximate factor determining their seasonal variation in physiology and activity.

Keywords: photoperiod; Anura; seasonality; assemblages; structural equation model; latent variables

Introduction

Organisms have evolved coupling of vital activities such as reproduction and migration, to specific moments of the year (Bradshaw and Holzapfel 2007). Several factors are suggested as potential causes of these rhythms in organisms' activity or abundance (called phenologies): tracking of seasonal resources, predator avoidance, positive interactions (facilitation), physiological constraints, temporal resource partitioning, as well as chance (Pianka 1973; Schoener 1974; Morin 1999; Richards 2002; Sandvik et al. 2002; Kronfeld-Schor and Dayan 2003; Bradshaw and Holzapfel 2007). The capacity to be ready for predictable events and to synchronize the physiology, biochemistry, and behaviour, promoting efficient organism function, can be determined by the response to external factors or by endogenous mechanisms (biological clocks) (Palmer 2002; DeCoursey 2004; Nelson 2005). As an external factor, photoperiod is a variable frequently used by organisms to predict the window of favourable conditions, for example to reproduce, mainly in temperate zones because

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ISSN 0022-2933 print/ISSN 1464-5262 online

DOI: 10.1080/00222930903377539
http://www.informaworld.com

of their predictable seasonal changes (Barrel et al. 2000; Dawson et al. 2001; Bradshaw and Holzapfel 2007).

Temperature and rainfall variables have been identified as the principal causes of annual activity cycles in amphibians because they are ectothermic animals with permeable skin and aquatic reproduction (Jørgensen 1992; Duellman and Trueb 1994; Stebbins and Cohen 1997; Hartel 2007). Rainfall has been proposed as the main factor regulating circannual anuran activity patterns in tropical regions, while a combination of temperature and rainfall has been suggested as the determinant in temperate regions (Duellman 1978; Duellman and Trueb 1994). Several empirical studies which tested this idea with monthly data of anuran calling activity, temperature, and rainfall arrived at contrasting results (Pombal 1997; Bernarde and dos Anjos 1999; Bernarde and Machado 2000; Prado et al. 2005; Afonso and Eterovick 2007).

Photoperiod is a climatic factor that gives relatively noise-free information about the time of the year and can be used by organisms as a cue of actual or future environmental conditions (Bradshaw and Holzapfel 2007). The evaluation of the potential role of photoperiod jointly with temperature and rainfall as determinants of anuran calling activity identified only the first variable as the determinant of activity (Both et al. 2008). Similarly, an additional study found that a model incorporating a sinusoidal effect of month explained up to 85% of the variation in anuran activity, outperforming rainfall and/or precipitation as explanatory variables (Canavero et al. 2008). However, Canavero et al. (2008) could not disentangle which component of the month was the cause of seasonal pattern of the anuran calling activity (e.g. photoperiod, biological clocks, complex of environmental variables) (Bradshaw and Holzapfel 2007). Both studies, Canavero et al. (2008) and Both et al. (2008), suggested that temperature and rainfall were not the main drivers of seasonal trends in anuran activity as had previously been suggested.

In this work we contrast the explanatory potential of a sinusoidal model that captures amphibian seasonality well with a model based on photoperiod. Further, we use a structural equation model to advance understanding of the underlying causal structure connecting the annual pattern of anurans' activity with the set of proposed determinants. Our analyses suggest that photoperiod plays a prominent role as the signal used by amphibians to synchronize their activity to annual variations in environmental conditions.

Materials and methods

Data

We monitored anuran activity at Espinas stream, Maldonado, Uruguay (34°47′S, 55°22′W) from September 1998 to April 2000. Every month we surveyed, during two-night fieldtrips, seven pre-defined sampling sites and registered the presence of each anuran species via acoustic identification of calling males (Zimmerman 1994) (for a detailed description of the study area and sampling design see Canavero et al. [2008]). To analyze the temporal structure of the anuran assemblage, we determined species richness (Table 1). The study area climate is "Cfa" of Köppen, warm temperate with an annual average temperature of 22.7°C (maximum) and 10.7°C (minimum), irregular rain, and an accumulated annual rainfall of 1100 mm. The

Table 1. Species richness, weather variables and photoperiod for the time series of the study area.

Sampling month	S	T	R	P	Res-Sin	Res-P
September 1998	4	12.5	8.6	12.3	0.21	0.23
October 1998	4	16.4	3.3	13.4	−1.34	−1.32
November 1998	6	17.9	12.4	14.2	−0.39	−0.44
December 1998	7	20.9	15.9	14.5	0.34	0.13
January 1999	7	20.8	21.1	13.9	0.93	0.98
March 1999	3	21.4	13.7	11.8	−0.15	−0.07
April 1999	2	15.9	6.2	10.8	0.40	0.34
May 1999	0	13.3	5.1	10.0	−0.55	−0.53
June 1999	0	10.6	10.3	9.8	−0.28	−0.25
July 1999	1	10.4	10.1	10.3	0.13	0.05
August 1999	3	12.3	10.1	11.2	0.85	0.78
September 1999	3	13.5	10.3	12.3	−0.79	−0.77
October 1999	7	15.6	6.1	13.4	1.66	1.68
November 1999	6	17.9	4.4	14.2	−0.39	−0.44
January 1999	6	22.8	1.7	13.9	−0.07	−0.02
February 1999	3	22.9	3.8	12.9	−1.79	−1.61
March 1999	5	20.2	8.6	11.8	1.85	1.93
April 1999	1	17.9	14.6	10.8	−0.60	−0.66

Notes: S, richness of calling males; T, mean monthly temperature; R, monthly rainfall; P, photoperiod; Res-P, residuals of the linear regression of the number of species calling per month (S) with photoperiod (Figure 2); Res-Sin, residuals of the sinusoidal model (Figure 3); T and R were obtained during the study period from the Carrasco International Airport weather station; P was calculated for each month with the Online-Photoperiod Calculator V1.97L (see Materials and Methods).

weather variables – mean monthly temperature and monthly rainfall – were obtained during the study period from the Carrasco International Airport weather station 60 km from the study area (Table 1). The photoperiod – number of light-hours at the time of the survey – was calculated with the Online-Photoperiod Calculator V1.97L (J. Lammi © 1996–2006: Computation of Daylengths, Sunrise/Sunset Times, Twilight and Local Noon http://tornio.info/sol.html).

Structural equation modelling

In order to advance our understanding of the potential causal structure connecting month as a latent variable, photoperiod, weather determinants – temperature and rainfall – and the number of anuran species in calling activity, we performed a path analysis. Structural equation modelling (SEM) was used to test the overall path diagram as a likely cause of observed data. SEM was based on maximum likelihood methods, working with the standardized variables which make comparable the relative importance of different paths. It should be noted that the interpretation of each path is the same as the coefficients associated to each variable in a multiple regression analysis. In addition, the explained variance for each endogenous variable was estimated as 1 minus the path coefficient between its associated error variable (represented with the symbol “u”) (Shipley 2000). Significance of the overall path model was assessed using the chi-squared (χ^2) statistic computed from the departure between the observed and expected covariance matrix from the proposed path model (Shipley 2000). In this analysis, a significant χ^2 ($p < 0.05$) value means that the model is not supported by the data. SEM has two basic assumptions: multivariate normality and linearity among variables. Our data satisfied both assumptions and no transformation was necessary. As a rule of thumb, path analysis requires a minimum of five observations for each independent path estimated in the model (Shipley 2000). Because we had 18 observations, we restricted our contrast of putative causal structures to models with no more than four causal links. The minimum number of measured variables needed per latent variable is four to fit and test a measurement model (Shipley 2000). In this vein, we developed an SEM evaluating the hypotheses that anuran species respond to time of year at a monthly scale as a latent variable which is a result of photoperiod, temperature and rainfall together. SEM makes a linear combination of these variables to build the latent variable (Shipley 2000). This latent variable encapsulates the main determinants of anuran activity that has been proposed, allowing the evaluation of their relative importance. Finally, we evaluated the linear correlation between photoperiod and number of anuran species calling per month and contrasted the explanatory potential of this variable with those presented by a sinusoidal model that well-represented anuran seasonality (Canavero et al. 2008).

Results

The latent variable – time of the year – was associated with the photoperiod (r = 1.00), temperature (r = 0.62), and community richness (r = 0.92). Rainfall did not bring information to the construction of the latent variable (Figure 1). This causal model accounted for 85% of the variation in richness (Figure 1), and no alternative model was congruent with the observations or significantly better than the reported one. The linear correlation between photoperiod and richness (S = –13.68 + 1.42*P, $R^2 = 0.85$, $p < 0.001$) (Figure 2) and the sinusoidal model developed by Canavero et al. (2008) (Figure 3) accounted for 85% of the variation (S = 3.47 + 3.20 sin[2π(M–0.63)/12], $R^2 = 0.85$, $p < 0.001$), the same amount of variation explained by the structural equation model presented in Figure 1. The number of anuran species with calling activity at a monthly scale was extremely well represented by photoperiod and to the same degree as by a sinusoidal model (Figures 1 and 2). Furthermore, the same pattern of residual variation is observed from these two approaches (y = 0.00 + 1.01*x, $R^2 = 0.99$, $p < 0.001$) (Figure 3).

Discussion

Plants and animals at temperate zones and extreme latitudes usually restrict their activity or life cycle to the time of the year where abiotic and biotic factors like temperature, food, predators and competitors are more appropriate (DeCoursey 2004; Nelson 2005). With few exceptions, activity in amphibian communities is typically seasonal (Donnelly and Guyer 1994) and it was previously considered that activity is determined by rainfall and/or temperature (Duellman and Trueb 1994, Stebbins and Cohen 1997). However, recent analyses challenged this view indicating that photoperiod (Both et al. 2008) or a combination of environmental variables (Canavero et al. 2008) could be the determinants of activity. There are ultimate factors that shape the

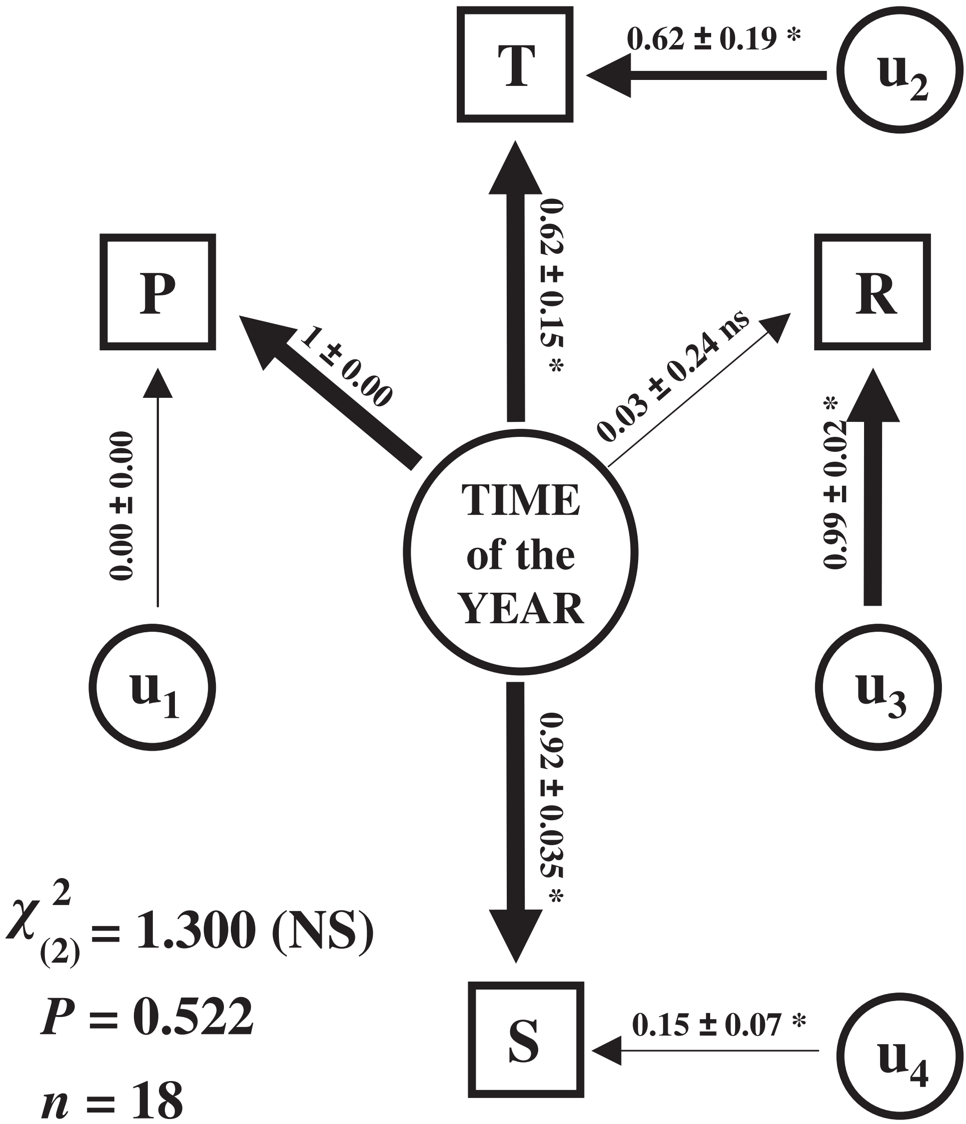

Figure 1. Path diagram of structural equation model, evaluating 265 the hypotheses that anuran species respond to the month as a latent variable that is a construct of photoperiod, temperature and rainfall. The whole model is congruent with observed data as indicated by its non-significant probability. Paths values are standardized effects ± 1 standard error. Asterisks (*) denote significant coefficients ($P < 0.05$) and "ns" denote non-significant coefficients ($P > 0.05$). Arrow width represents the strength of the causal link. Month, latent variable; S, number of species calling per month; P, photoperiod; T, mean monthly temperature; R, monthly rainfall; u1 to u4, associated error variable.

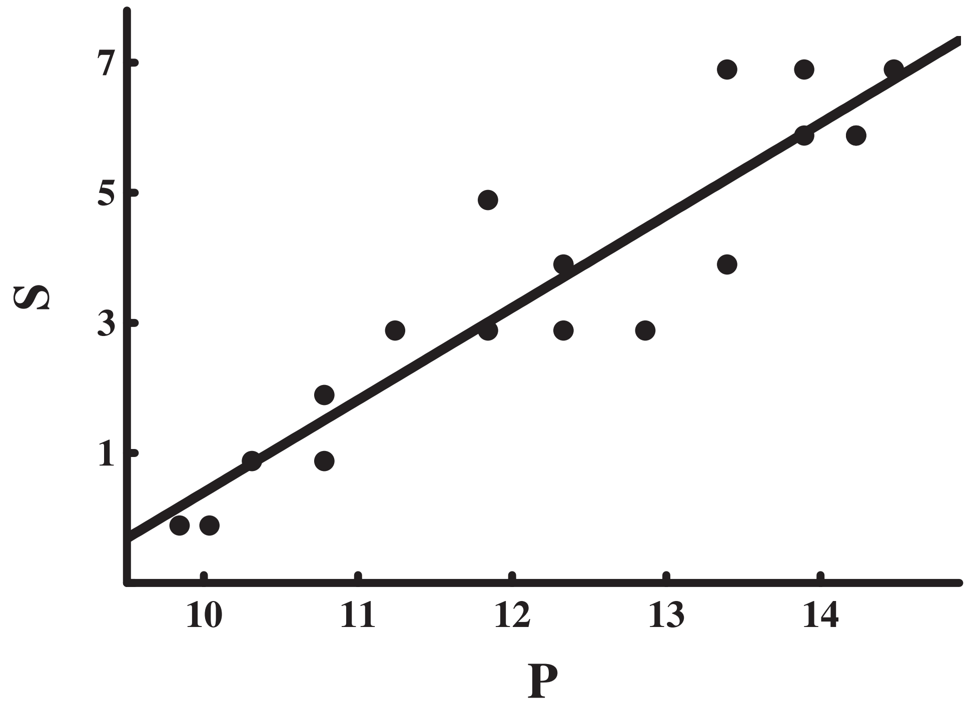

Figure 2. Linear regression of the number of species calling per month (S) between September 1998 and April 2000 with photoperiod (P).

evolution of biological seasonality (e.g., competition, predation, temperature, physiological restrictions), and proximate factors that supply the direct stimuli for the physiological regulation of the biological seasonality (e.g., photoperiod, biological clocks). Photoperiod is the variable most commonly used by organisms to predict a window of favourable conditions, particularly to reproduce, because it gives noise-free information about the time of the year (Bradshaw and Holzapfel 2007). Finally, it should be highlighted that the poor performance of precipitation and/or temperature against photoperiod as determinants of amphibian activity, and the wide use of this last environmental cue in very different organisms, indicates photoperiod to be the most plausible variable leading to seasonal variation in amphibian activity.

The use of SEM allows the translation of a set of hypotheses on the functioning of a system into a causal structure and their evaluation as a likely cause of observed data (Shipley 2000). We constructed and evaluated a latent variable – time of the year – that synthesized the seasonality of the system in temperature, photoperiod, and species richness but excluded, computationally, rainfall as a component of congruent seasonal variation. This agrees with the idea that in those regions where rainfall is uniform or irregular throughout the year, amphibians will follow climatic factors that are truly seasonal (Both et al. 2008). The additional contribution of the SEM is the identification of the connection between photoperiod and the latent variable that represents temporal dynamics of the main variables of our study system. Conditions to observe a path coefficient of exactly 1 and associated error equal to 0 are notably

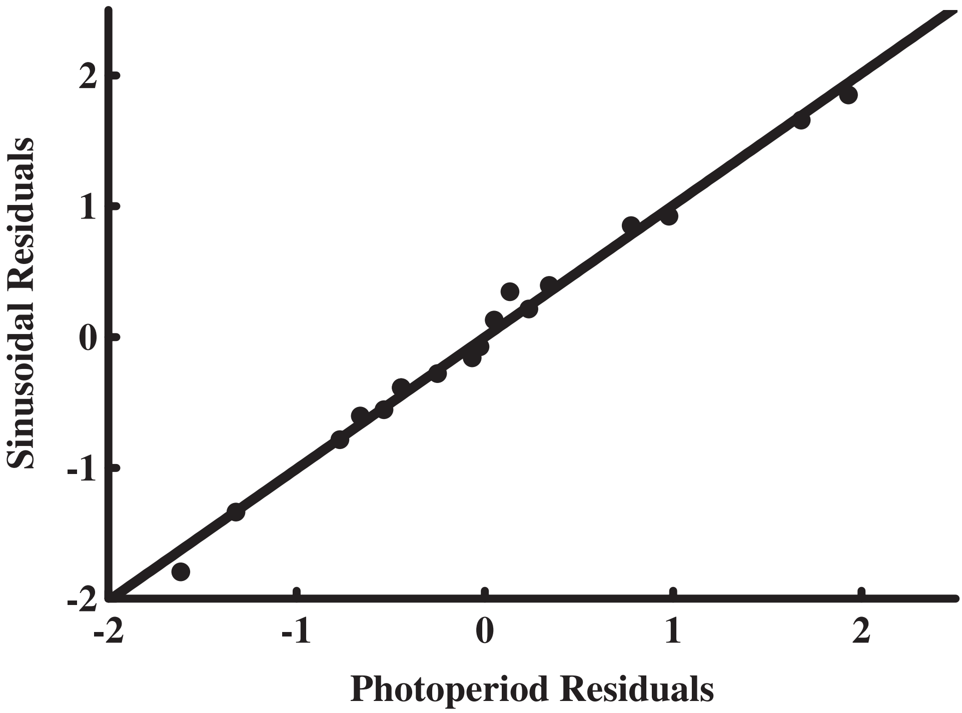

Figure 3. Correlation between residuals of the regression between photoperiod and amphibian activity and the fit of the sinusoidal model.

restricted and imply that the same set of observations are represented by the two variables. In this case, with a latent variable involved, which is reconstructed with information of several observed variable, the estimated coefficient and associated error indicate that photoperiod is exactly reproducing the co-variation among the other variables that is summarized in the latent variable. Consequently, this represents strong support for a potential role of photoperiod as the variable used by amphibians to regulate their activity. This is reinforced by the fact that the sinusoidal nature of amphibians' activity, estimated without consideration of photoperiod, captured exactly the same trend that is estimated when a single linear regression with photoperiod is fitted. The sinusoidal and the linear model capture the same information not only because of the congruence in explained variance, but because the same pattern of residuals is observed in both analyses. The fact that photoperiod is capable of capturing this seasonal dynamic in an identical way is a strong support for both the sinusoidal model which represents seasonality and to photoperiod as the most plausible variable behind amphibian seasonal activity.

The potential role of photoperiod is further supported by the identification of its physiological effects on amphibians. Amphibians can sense the seasonal variation of the day length by melatonin hormone segregation and use this signal to couple physiological processes and behavioural patterns with time (Jørgensen 1992; D'Istria et al. 1994; Bradshaw and Holzapfel 2007; Both et al. 2008). The use of an environmental signal to adjust behaviour and physiology with time, requires the existence of a mechanism connecting the signal with the organism's physiology. At least with melatonin this mechanism has been shown to be present in amphibians, supporting the use of photoperiod as a main environmental signal of time (Jørgensen 1992; D'Istria et al. 1994; Bradshaw and Holzapfel 2007).

The claim for a main role of photoperiod determining annual amphibian activity requires consideration of the statistical association between this activity and temperature and precipitation reported elsewhere (Cardoso and Martins 1987; Donnelly and Guyer 1994, Oseen and Wassersug 2002; Gottsberger and Gruber 2004; Saenz et al. 2006). This association is expected when the analysis is realized at smaller temporal scales, in particular in tropical communities where photoperiod is less informative or because of the existence of a strong association between photoperiod and temperature or precipitation (Oseen and Wassersug 2002; Gottsberger and Gruber 2004; Saenz et al. 2006). Our analysis explores an 18-month time series with a monthly grain. At this scale, photoperiod arises as the main stimulus that the anuran community tracks shaping the observed sinusoidal pattern of activity. However, at small temporal scales (e.g. days or weeks) some authors have found that temperature and rainfall stimulate or even constrain anuran activity (Cardoso and Martins 1987; Donnelly and Guyer 1994; Oseen and Wassersug 2002; Gottsberger and Gruber 2004; Saenz et al. 2006). In this sense, our results and those presented elsewhere are congruent but operate at different scales (Cardoso and Martins 1987; Donnelly and Guyer 1994; Oseen and Wassersug 2002; Gottsberger and Gruber 2004; Saenz et al. 2006). Although non-seasonal activity patterns in tropical amphibian communities are theoretically plausible, the fact is that most communities are strongly seasonal in their activity (Canavero et al. 2009). At the tropics, where photoperiod is relatively constant all year round, other variables like precipitation or food availability may operate as the seasonal cue (DeCoursey 2004; Goldman et al. 2004; Nelson 2005). Finally, photoperiod is usually associated with climatic variables such as temperature and precipitation (Bradshaw and Holzapfel 2007). As a consequence, the observed association between climatic variables and amphibian activity could originate because of their association with photoperiod but not due to the existence of a causal link between them. In a statistical sense, these climatic variables operate as proxy variables of photoperiod (Shipley 2000). In this work we have challenged the classical ideas which identify temperature and rainfall as the main variables that determine annual activity patterns of anuran communities (Blair 1961; Berry 1964; Duellman 1978; Rossa-Feres and Jim 1994; Pombal 1997). An understanding of the development and maintenance of anuran temporal activity patterns lies in the elucidation of the underlying mechanisms, which could be operating at different scales (Levin 1992; Maurer 1999; Angilletta et al. 2006). The wide use of photoperiod by different organisms as a signal to breed, the previous identification of amphibians' physiological response to photoperiod, and the results presented in this paper, support a major role for photoperiod as a signal used by amphibians to track seasons.

Acknowledgements

We thank A. Camargo, I. da Rosa, R. Maneyro, and D. E. Naya for help on fieldwork and comments on data interpretation, M. Root-Bernstein and A. Camargo for contributions on English editing. This article was fund by a grant of Programa de Desarrollo de las Ciencias Básicas (PEDECIBA, Uruguay) to AC. MA is grateful for the support of Progama de

Desarrollo Tecnológico (PDT 71-10) and FONDECYT-FONDAP grant 1501-0001 (Programs 2). We are very grateful to three anonymous reviewers for their comments on an earlier version of this manuscript. AC is very grateful to E. Castiñeira without her support this work would not have been possible.

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