

Interspecific variation in the phenology of advertisement calling in a temperate Australian frog community

Geoffrey W. Heard^{1,2}, Stefano Canessa¹ & Kirsten M. Parris³

¹School of BioSciences, The University of Melbourne, Parkville, Victoria 3010, Australia

²Department of Biology, University of York, Wentworth Way, York YO10 5DD, UK

³School of Ecosystem and Forest Sciences, The University of Melbourne Burnley Campus, 500 Yarra Boulevard, Richmond, Victoria 3121, Australia

Keywords

Amphibian, Australia, coexistence, niche, partitioning, phenology.

Correspondence

Geoffrey W. Heard, School of BioSciences, The University of Melbourne, Victoria, Australia 3010. Tel: +44 7985 510920; Fax: +44 1904 328505; E-mail: heardg@unimelb.edu.au

Present address

Stefano Canessa, Institute of Zoology, Zoological Society of London, Regents Park, London NW1 4RY, UK

Funding Information

Funding was provided by the Australian Research Council, Australian National Environmental Research Program, Australian Research Centre for Urban Ecology, Victorian Department of Environment, Land, Water and Planning, Growling Grass Frog Trust Fund, Museums Victoria, Melbourne Water, Parks Victoria and the Victorian Department of State Development, Business and Innovation.

Received: 10 May 2015; Revised: 13 July 2015; Accepted: 22 July 2015

Ecology and Evolution 2015; 5(18): 3927–3938

doi: 10.1002/ece3.1666

Introduction

Niche partitioning in ecological communities may entail differential responses to a large number of environmental axes (Hutchinson 1957). This partitioning is often considered in spatial terms, but the partitioning of resources through time can also facilitate the coexistence of ecologically similar species (Townsend et al. 2008). Evidence of temporal partitioning may be found at various scales,

Abstract

Spatial and temporal partitioning of resources underlies the coexistence of species with similar niches. In communities of frogs and toads, the phenology of advertisement calling provides insights into temporal partitioning of reproductive effort and its implications for community dynamics. This study assessed the phenology of advertisement calling in an anuran community from Melbourne, in southern Australia. We collated data from 1432 surveys of 253 sites and used logistic regression to quantify seasonality in the nightly probability of calling and the influence of meteorological variables on this probability for six species of frogs. We found limited overlap in the predicted seasonal peaks of calling among these species. Those shown to have overlapping calling peaks are unlikely to be in direct competition, due to differences in larval ecology (*Crinia signifera* and *Litoria ewingii*) or differences in calling behavior and acoustics (*Limnodynastes dumerilii* and *Litoria raniformis*). In contrast, closely related and ecologically similar species (*Crinia signifera* and *Crinia parinsignifera*; *Litoria ewingii* and *Litoria verreauxii*) appear to have staggered seasonal peaks of calling. In combination with interspecific variation in the meteorological correlates of calling, these results may be indicative of temporal partitioning of reproductive activity to facilitate coexistence, as has been reported for tropical and temperate anurans from other parts of the globe.

from differing activity times within the diel cycle (Kronfeld-Schor and Dayan 2003), to interspecific variation in reproductive effort between years (Silvertown 2004). However, differences in phenology are the most familiar forms of temporal partitioning within ecological communities. Here, examples include sympatric mantids whose annual life cycles are staggered to allow coexistence (Hurd and Eisenberg 1989) and temporal segregation of larval development in odonate communities to reduce

competitive and predatory interactions (Crowley and Johnson 1982).

In communities of amphibians, interspecific variation in reproductive phenology and its implications for coexistence has received some attention, particularly for species whose reproductive activity can be tracked by male advertisement calls (Wells 2007). Advertisement calling is exhibited by most species of frogs and toads. Within species, calls convey information about the location and fitness of males to prospective partners and competitors; among species, calls evolve distinct acoustics that act as an important premating isolation mechanism (Wells 2007). However, phenological differences also represent a key source of interspecific variation in advertisement calling in anuran communities, signaling considerable variation in the timing of reproduction.

In tropical environments, calling occurs primarily during the rainy season, but there may be considerable heterogeneity in the timing of calling linked to the wide variety of reproductive modes displayed. For example, among 31 species of frogs studied by Gottsberger and Gruber (2004) in French Guiana, species could be characterized as obligate early season callers (species that lay foam nests or display direct development), mid- or late season callers (species with embryonic development over water), sporadic and explosive callers (species that lay eggs directly into water), or generalists that call right through the rainy season (species with parental care of larvae). A comparable diversity of strategies has been reported for other tropical anuran communities, including species that call exclusively during the dry season (Aichinger 1987; Donnelly and Guyer 1994; Bertoluci 1998; Bertoluci and Rodrigues 2002). Temperate anurans may also vary substantially in calling seasonality. Among 13 species in eastern Texas, Saenz *et al.* (2006) documented calling seasons ranging from 2 to 12 months. In Ontario, de Solla *et al.* (2006) monitored a community of eight species and found little or no overlap in the calling seasons of several taxa.

Sympatric anurans can also vary markedly in their meteorological cues for calling. Even among aquatic-breeding amphibians from the same community, responses to rainfall can vary considerably, from explosive initiation of calling in response to rain, to dampening or even cessation of calling in response to rain (Oseen and Wassersug 2002; Gottsberger and Gruber 2004; Saenz *et al.* 2006). Positive and negative relationships between environmental temperature and calling activity are also known in anuran communities, with some species favoring warm conditions and others cooler conditions (Gottsberger and Gruber 2004; Steelman and Dorcas 2010). Similarly, while the fundamental effects of relative humidity and wind strength on water balance and thermoregulation in

anurans (Tracy 1976) suggest that the former should be positively correlated with calling activity and the latter negatively, the relationship between these variables and calling may be idiosyncratic (Oseen and Wassersug 2002).

While it is clear that the phenology of calling can vary widely within anuran communities, it is also true that the available data on the subject are overwhelmingly derived from anuran communities in the Americas (Wells 2007). Few, if any, studies are available for large parts of Africa and Eurasia. The same is true for Australia. Of the 241 frogs so far described in Australia (Anstis 2013), only nine species (4%) have been the focus of dedicated phenological studies on calling and reproduction to our knowledge (MacNally 1984; Williamson and Bull 1992; Driscoll 1998; Brooke *et al.* 2000; Lemckert 2001; Hollis 2003; Wong *et al.* 2004; Hauselberger and Alford 2005; Canessa *et al.* 2012). Likewise, we are aware of only seven studies of the phenology of calling across an Australian frog community (Humphries 1979; Gillespie 2001; Morrison 2001; Lemckert and Mahony 2008; Lemckert and Grigg 2010; Dostine *et al.* 2013; Lemckert *et al.* 2013).

Here, we describe the phenology of advertisement calling in an anuran community from the temperate climes of southern Australia, focusing on interspecific variation in both the seasonality of calling and the meteorological cues for calling. We combined data collected over 11 years to develop models of the nightly probability of calling by the focal species. As has been documented for tropical and temperate anuran communities elsewhere, our data reveal considerable interspecific variation in the seasonality of calling and the weather conditions that favor calling, which may be indicative of temporal partitioning of reproductive activity in this community.

Methods

Study sites and surveys

We conducted 1432 nocturnal surveys for frogs between 2001 and 2012 at 253 sites across the volcanic plains north and west of Melbourne, Victoria, Australia. Sites were distributed in the catchments of the Darebin, Merri, Moonee Ponds, and Kororoit Creeks. The landscape is undulating, rising to a maximum elevation of ~300 m asl at the study sites. Upper catchments are dominated by grazing land, graduating to industrial and urban estates in the lower catchments. The climate is temperate, with cool winters (July mean daily temperature range = 5.4–13.1°C) and warm summers (February mean daily temperature range = 14.1–26.6°C) (BOM 2014). Rainfall averages 538 mm, with the highest monthly rainfall occurring in late winter and spring (August–November) in most years (BOM 2014).

Sites included slow flowing pools along the main channel and tributaries of the streams listed above, as well as lentic wetlands such as farm dams, flooded quarries, swamps, and water treatment ponds. Site selection was haphazard, including both randomized protocols (mostly for selecting pools along streams) and nonrandomized protocols that aimed to maximize geographic coverage while accounting for both access and logistical constraints (for further details, see Canessa et al. 2012; Canessa and Parris 2013; Heard et al. 2015).

Surveys were conducted between September and April (inclusive) in each year, encompassing the Austral spring, summer, and autumn. Survey timing sought to optimize detection rates of *Litoria raniformis* in most cases; this endangered species having been studied intensively in this region since 2001 (Heard et al. 2012a,b, 2013, 2015). However, aural surveys during the spring and early summer months optimize detection rates across the frog community in this region (Canessa and Parris 2013). Survey techniques were broadly consistent between sites and years. Surveys commenced at least 30 min after dark and began with a period of 5–10 min listening quietly for male advertisement calls. Frogs in the study area have distinctive calls that allow ready identification to species. Sites were then searched on foot with the aid of spotlights. Any additional calls heard during these searches were recorded. Surveys extended up to 265 min, with up to 10 repeat surveys at a site in any given year. Surveys were completed under permits 10001816, 10003005, and 10005649 issued by the Victorian Department of Environment, Land, Water and Planning.

To supplement the above survey dataset, we collated data from 263 nocturnal surveys for frogs completed at the same study sites in the same period by private consultants, other researchers, and local naturalists. All surveys were conducted during the Austral spring, summer, or autumn, and followed surveys protocols analogous to our own. Survey data were gathered from the relevant research report or thesis, or through personal communications. Full details are provided by Heard et al. (2015).

Meteorological variables

Six meteorological variables were considered as potential determinants of calling activity. Air temperature (dry bulb, °C) and relative humidity (%) were recorded during most surveys with the aid of a compact whirling hygrometer (Brannan P/L, Cumbria, UK). Surface water temperature was recorded using a digital probe thermometer (varying brands). Wind strength was recorded subjectively on an ordinal scale between 0 (still) and 3 (strong, regular gusts). Rainfall (mm) was derived from the Australian Bureau of Meteorology (BOM 2014), taking measure-

ments from the Melbourne Airport weather station, located roughly in the center of the study area (-37.67 S, 144.83 E). Two measures of rainfall were used: rainfall on the day of the survey and cumulative rainfall over the preceding 7 days (“lagged” rainfall).

Modeling

We used Bayesian logistic regression to model the nightly probability of calling for those species with a sufficient number of detections. For each of these species, we began by filtering the nondetection data to exclude records from sites in years when no detections of calling were made. Hence, for each species, only detection and nondetection data from sites that were known to be occupied by reproductively active males in a given year were included. We also removed any surveys when the focal wetland was dry (which precludes calling among the focal species) and randomly filtered the remaining dataset for each species such that only one site was included for any given survey night. Repeat surveys of the same site in a given year were assumed to be independent. Hence, for each species, the detection (1) or nondetection (0) of calling on survey night i at a site known to be occupied by reproductively active males was treated as a Bernoulli variable with probability p_i .

Covariate effects on p_i were modeled using a logistic equation and linear link function:

$$\log\left(\frac{p_i}{1-p_i}\right) = \alpha + \sum \beta_x \cdot X_i, \quad (1)$$

where α is the intercept, and β_x is the regression coefficient for covariate X . The underlying seasonal variation in p_i was modeled using a Fourier series approach following Burnham and Anderson (2002, p. 188). The approach treats phenomena as displaying a regular pattern that may be described using cosine functions of increasing complexity. We chose a simple two parameter version. The change in p_i with days since the start of the Austral spring (September 1, days _{i}) was modeled as:

$$\log\left(\frac{p_i}{1-p_i}\right) = \alpha + \beta_1 \cdot \cos\left(\frac{2\pi \cdot \text{days}_i}{365}\right) + \beta_2 \cdot \sin\left(\frac{2\pi \cdot \text{days}_i}{365}\right). \quad (2)$$

With the exception of wind strength (which did not show any obvious seasonality), raw meteorological data for each survey were first adjusted to represent the anomaly from the seasonal mean. After Canessa et al. (2012), we fitted up to fourth degree polynomial regressions

between each meteorological variable and survey date using maximum likelihood in *R* version 3.0.3 (R Core Team 2014). The best-fitting model for each meteorological variable was selected using Akaike's information criterion (Burnham and Anderson 2002), and the residuals from this model used as inputs for the logistic models.

Fourteen models of p_i were fitted to the detection data for each species. Each model contained one of the two rainfall variables, plus one or more of temperature, relative humidity, and wind strength. Models were fitted twice for each species; once with temperature represented by air temperature and once with temperature represented by water temperature. The best-fitting temperature variable for each species was selected based on model selection statistics. Correlations between predictors were weak in the model set (Pearson's r correlations ranged from -0.13 to 0.25), except for a moderate negative correlation between air temperature and humidity (Pearson's r of -0.46). An effect of survey effort (survey duration multiplied by the number of observers) was included in all models to account for the fact that the probability of detecting males that are calling sporadically increases with survey duration, and multiple surveyors have a higher cumulative chance of hearing sporadic or weakly calling individuals. A random "year" effect was also included to account for annual variation in calling activity.

Models were fitted to the data using Markov Chain Monte Carlo (MCMC) sampling in *OpenBUGS* version 3.2.3 (Thomas et al. 2006), called from *R*. Uninformative priors were used for each parameter. With the exception of survey date, covariates were centered by subtracting the mean and dividing by two standard deviations. Parameter estimates and their 95% credible intervals (95% CI) were drawn from 40,000 MCMC samples after a burn-in of 60,000 samples. Models were compared using the deviance information criterion (Spiegelhalter et al. 2002). The best-fitting model for each species was used to predict their nightly probability of calling across 366 days, beginning and ending on September 1. In turn, these predictions were used to estimate the seasonal peak in the probability of calling for each species.

Results

Eight frog species were detected during this study: *Crinia signifera*, *Crinia parinsignifera*, *Limnodynastes dumerilii*, *Limnodynastes tasmaniensis*, *Litoria ewingii*, *Litoria peronii*, *Litoria raniformis*, and *Litoria verreauxii*. Six species were commonly detected: *C. signifera* (396 detections total, 177 detections on independent nights), *Lim. dumerilii* (184 total, 95 independent), *Lim. tasmaniensis* (318 total, 165 independent), *Lit. ewingii* (132 total, 79 independent), *Lit. raniformis* (210 total, 120 independent), and *Lit. ver-*

reauxii (87 total, 49 independent). *Crinia parinsignifera* and *Lit. peronii* were detected on only three and eight occasions, respectively.

Although there was considerable temporal overlap in calling activity (Fig. 1), the seasonality and predicted peak of calling varied among species (Figs. 2, 3). Of 15 possible species-to-species comparisons of the predicted peak in the nightly probability of calling, the 95% credible intervals overlapped in only four cases (*C. signifera* & *Lim. tasmaniensis*; *C. signifera* & *Lit. ewingii*; *Lim. dumerilii* & *Lit. raniformis*; *Lim. tasmaniensis* & *Lit. verreauxii*; Fig. 3).

Crinia signifera and *Lit. ewingii* were recorded calling in all survey months, but most frequently in early spring (Fig. 1). For these species, the estimated seasonal peak of calling was in July (Fig. 3), with a steep decline in the nightly probability of calling from November to February, followed by a rapid recovery during autumn (Fig. 2). *Limnodynastes tasmaniensis* displayed a similar (although weaker) pattern, with observed calling in all survey months (Fig. 1), but an estimated peak in the nightly probability of calling in September and trough in March (Figs. 2, 3). *Litoria verreauxii* is primarily a spring breeder. For this species, the proportion of surveys in which calling was detected declined in a roughly linear fashion after September (Fig. 1); however, the estimated seasonal peak in the probability of calling was in October (Fig. 3). Thereafter, the nightly probability of calling declined sharply, reaching near zero in mid-autumn (Fig. 2). *Limnodynastes dumerilii* and *Lit. raniformis* displayed the closest pattern of calling activity. The nightly probability of calling was estimated to peak in early December for both species (Fig. 3), before declining to zero or slightly thereabouts during autumn and winter (Fig. 2). *Crinia parinsignifera* and *Lit. peronii* were only detected calling between November and early February.

Interspecific variation was also apparent in relationships between the nightly probability of calling and the meteorological variables considered (Tables 1, 2). Relatively high rainfall in the preceding 7 days increased the probability of calling by *C. signifera*, *Lim. dumerilii*, *Lim. tasmaniensis*, and *Lit. ewingii* (Table 2). However, there was a clear negative effect of lagged rainfall on the probability of calling by *Lit. raniformis* (mean estimate = -0.60 , 95% CI = -1.10 , -0.11 ; Table 2). Likewise, while the probability of calling by both *Lim. dumerilii* and *Lit. raniformis* increased as the temperature anomaly increased, the former responded more strongly to air temperature, while the latter responded to water temperature (Tables 1, 2). Relative humidity was only related to the probability of calling for *Lit. ewingii* and *Lit. verreauxii*, having a positive effect in both cases (*Lit. ewingii*: mean estimate = 1.15 , 95% CI = 0.39 , 1.96 ; *Lit. verreauxii*: mean estimate = 1.1 , 95% CI = 0.06 , 2.22 ; Table 2).

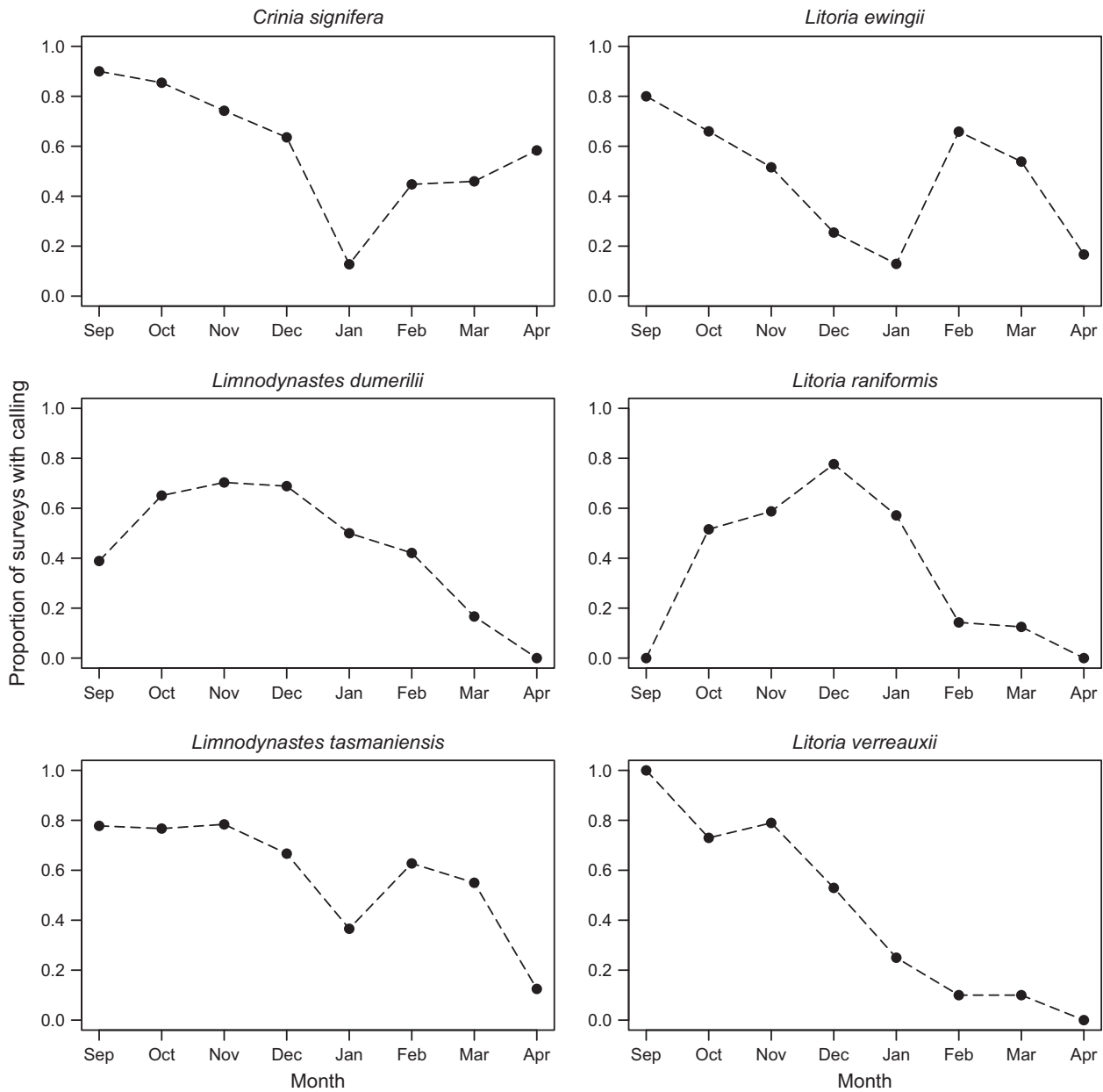


Figure 1. The proportion of surveys in each month during which calling was recorded for the six commonly detected species. Only surveys at sites that were known to be occupied in a given year are included for each species (calling was detected at least once at those sites in those years).

Discussion

There are two obvious mechanisms through which temporal partitioning of reproductive effort may facilitate coexistence in anuran communities. The first is reducing acoustic competition. Intraspecifically, male anurans compete acoustically for mates in various ways, including extrinsic factors such as caller location (Littlejohn 1977;

Parris 2002) and intrinsic factors such as call duration and acoustic frequency (Littlejohn 1977; Wagner 1992; Welch et al. 1998). Interspecifically, acoustic competition may arise purely through interference (Littlejohn 1977). For example, Littlejohn and Martin (1969) demonstrated inhibition of calling by *Pseudophryne semimarmorata* in direct response to acoustic interference from sympatric *Geocrinia victoriana* in southern Australia. Likewise,

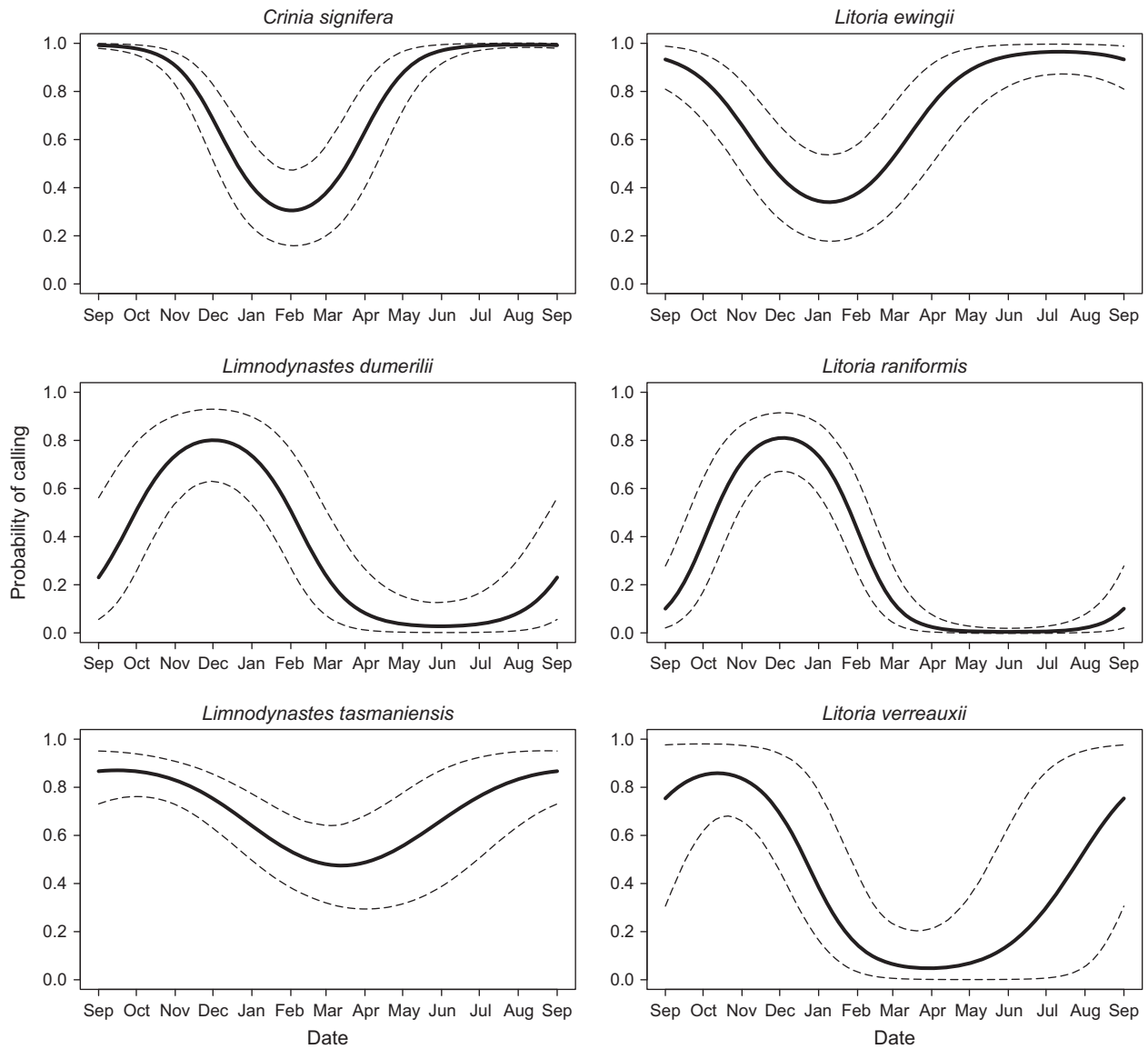


Figure 2. The estimated nightly probability of calling over 366 days for the six commonly detected species, beginning and ending on the September 1. Estimates are taken from the top model for each species and assume that all other variables influencing the detection of calls (meteorological variables and survey effort) are at their mean values. Models were fitted to survey data from sites that were known to be occupied in a given year (calling was detected at least once at those sites in those years). Solid lines show the mean estimates and the dashed lines the 95% CIs.

Schwartz and Wells (1984) reported reductions in the attractiveness of calls of *Hyla ebraccata* in Panama when the primary notes overlapped with calls of the sympatric *H. microcephala*. In an extensive study of 39 species across three anuran communities in Brazil, Duellman and Pyles (1983) demonstrated considerable overlap in the acoustic properties of calls. They concluded that temporal partitioning of calling, both in terms of the seasonal timing and environmental conditions under which calling takes place, was an important mechanism by which acoustic

interference is mitigated (and coexistence facilitated) in these communities.

The second mechanism by which partitioning of reproductive phenology may facilitate coexistence in anuran communities is mitigation of larval competition. Competitive interactions between larval anurans are a key determinant of larval survival and metamorphic success (Alford 1999). Resource competition among larvae also has important carry over effects on the fitness and survival of postmetamorphic anurans (Chelgren *et al.* 2006).

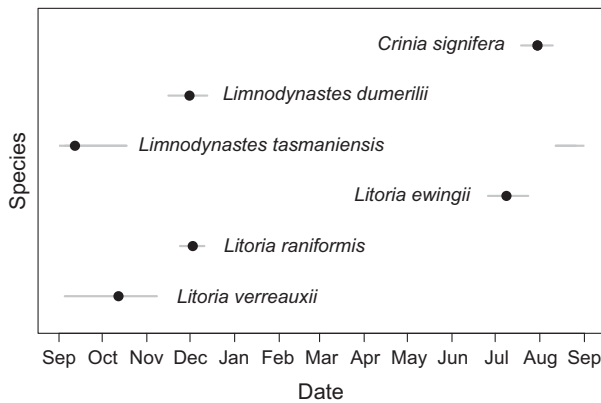


Figure 3. The estimated seasonal peak of the nightly probability of calling for the six commonly detected species. Dots are the means and the gray lines the 95% CIs. Estimates are taken from the top model for each species and assume that all other variables influencing the detection of calls (meteorological variables and survey effort) are at their mean values.

Hence, larval competition represents a key determinant of anuran population dynamics and community structure (Wells 2007).

The early work of Alford and Wilbur on the subject of larval competition in anuran communities produced evidence both for and against temporal partitioning as a mechanism for coexistence (Alford and Wilbur 1985; Wilbur and Alford 1985; Alford 1989a,b). Temporal partitioning was important for the outcomes of some interactions (Alford and Wilbur 1985; Wilbur and Alford 1985; Alford 1989a), but not others (Alford 1989b). Later work confirmed that the strength of larval competition between species varies intrinsically, and mediates the importance of temporal partitioning for larval fitness (Gascon 1992). It also showed that the temporal order in which interactions take place (so-called “priority effects”) may be an important determinant of the strength of competitive interactions among anuran larvae (Lawler and Morin 1993).

We cannot demonstrate that the interspecific variation in calling phenology documented here is adaptive with regard to coexistence, but there are several interesting points to be made in this regard. In the focal community, two species pairs could be expected to benefit most from partitioning of reproductive phenology: *Lit. ewingii* & *Lit. verreauxii* and *C. signifera* & *C. parinsignifera*. These frogs are closely related, have analogous larval ecologies and similar advertisement calls (Loftus-Hills 1973; Watson et al. 1985; Anstis 2013). *Litoria ewingii* and *Lit. verreauxii* also occasionally hybridize (Watson et al. 1985; Smith et al. 2012). Our data suggest that *Lit. ewingii* and *Lit. verreauxii* display subtle differences in their seasonal calling peak, with *Lit. ewingii* being primarily a winter breeder

and *Lit. verreauxii* having a calling peak in early to mid-spring. However, there was considerable uncertainty surrounding our estimates of calling seasonality for *Lit. verreauxii*, and we note that an earlier, winter peak in calling activity has been recorded elsewhere for this species (Humphries 1979; Smith et al. 2003; Lemckert and Grigg 2010). Nevertheless, these studies of *Lit. verreauxii* generally took place in allopatry from *Lit. ewingii*. The lagged peak in calling for *Lit. verreauxii* suggested by our study could be indicative of temporal partitioning when in sympatry with *Lit. ewingii*. Our data are very limited for *C. parinsignifera*; however, they suggest that the peak calling period of *C. parinsignifera* occurs later than that of *C. signifera*, and this agrees with observations elsewhere (Humphries 1979; MacNally 1979). Indeed, MacNally (1979) reported that *C. signifera* truncates its spring calling period to minimize overlap with *C. parinsignifera* when the two species occur in sympatry.

It is also notable that the species pairs with the closest seasonal patterns of calling activity – *C. signifera* & *Lit. ewingii* and *Lim. dumerilii* & *Lit. raniformis* – display traits that should weaken competitive interactions. Tadpoles of *C. signifera* and *Lim. dumerilii* are bottom feeders, whereas those of *Lit. ewingii* and *Lit. raniformis* tend to feed higher in the water column (Anstis 2013; pers. obs.). As such, resource competition between larval *C. signifera* and *Lit. ewingii* and between larval *Lim. dumerilii* and *Lit. raniformis* may be limited. Likewise, while *C. signifera* and *Lit. ewingii* call over a similar frequency band (Parris et al. 2009), the former calls from concealed positions under vegetation or crevices, while *Lit. ewingii* generally calls from elevated positions in vegetation (pers. obs.). Elevated perches can significantly increase the effective distance of calls (Parris 2002); hence, acoustic interference of *Lit. ewingii* by *C. signifera* may be mitigated by microhabitat partitioning. Different caller positions may also mitigate acoustic interference between *Lim. dumerilii* and *Lit. raniformis*; *Lim. dumerilii* calls from hidden positions under banks and rocks, or in emergent vegetation (Anstis 2013; pers. obs.), whereas *Lit. raniformis* calls primarily from mats of aquatic vegetation (Heard et al. 2008; pers. obs.). These two species also favor slightly different meteorological conditions for calling, and their calls differ acoustically (dominant frequency of 680 Hz for *Lim. dumerilii* vs. 1200 Hz for *Lit. raniformis*; Loftus-Hills 1973).

Our data revealed both expected and unexpected relationships with regard to the meteorological correlates of calling in this community. The probability of calling increased with increasing rainfall over the preceding 7 days for *C. signifera*, *Lim. dumerilii*, *Lim. tasmaniensis*, and *Lit. ewingii*. None of these species displayed strong relationships with rainfall on the day of survey. Hence,

Table 1. The five top-ranked models of the nightly probability of calling for the six commonly detected species. All models include cosine effects of days since September 1 and a linear effect of survey effort (to account for the fact that the probability of detecting calls increases with effort). Dots show the meteorological variables included in each model. They are as follows: air or water temperature anomaly (Temp), humidity anomaly (Hum), wind strength (Wind), rainfall anomaly (mm) either for the day of survey (Rain) or for the preceding 7 days (Rain lag). Model selection statistics are the deviance information criterion (DIC), distance from the top model (Δ DIC), and model weight (w).

Species	Temp	Hum	Wind	Rain	Rain lag	DIC	Δ DIC	w
<i>Crinia signifera</i>		●			●	295.20	0.00	0.30
			●		●	295.90	0.70	0.21
	●				●	296.10	0.90	0.19
	●		●		●	297.30	2.10	0.10
	●	●			●	297.80	2.60	0.08
<i>Limnodynastes dumerilii</i> ¹	●	●			●	188.90	0.00	0.38
	●				●	189.50	0.60	0.28
	●		●		●	191.50	2.60	0.10
	●	●	●		●	191.60	2.70	0.10
		●			●	192.70	3.80	0.06
<i>Limnodynastes tasmaniensis</i>		●			●	280.30	0.00	0.30
	●	●			●	282.00	1.70	0.13
	●				●	282.20	1.90	0.12
		●	●		●	282.50	2.20	0.10
			●		●	282.60	2.30	0.09
<i>Litoria ewingii</i> ¹		●			●	225.80	0.00	0.41
	●	●			●	227.30	1.50	0.19
		●	●		●	227.50	1.70	0.18
	●	●	●		●	228.10	2.30	0.13
			●		●	231.20	5.40	0.03
<i>Litoria raniformis</i>	●				●	254.40	0.00	0.36
	●		●		●	255.80	1.40	0.18
	●	●			●	256.50	2.10	0.13
	●			●		256.70	2.30	0.12
	●	●	●		●	257.70	3.30	0.07
<i>Litoria verreauxii</i> ¹		●			●	103.30	0.00	0.20
		●				103.40	0.10	0.19
	●	●			●	104.30	1.00	0.12
	●	●		●		104.80	1.50	0.09
		●	●		●	105.60	2.30	0.06

¹Temp is air temperature for these species.

the influence of rainfall on calling activity is most likely mediated by its effect on wetland water levels, as is often the case for aquatic-breeding anurans (Wells 2007). In contrast, rainfall curtailed calling activity by *Lit. raniformis*. Although somewhat counterintuitive, this relationship has been reported for ecologically analogous ranid frogs from North America. Saenz *et al.* (2006) demonstrated a negative relationship between calling activity and rainfall for both *Lith. catesbeiana* and *Lith. clamitans* in eastern Texas. *Lit. raniformis*, *Lith. catesbeiana*, and *Lith. clamitans* are all largely aquatic, summer breeding frogs that occupy permanent wetlands (Heard *et al.* 2008, 2013; Saenz *et al.* 2006; this study). They also all favor nights with warmer water temperatures for calling (Oseen and Wassersug 2002; Saenz *et al.* 2006; this study). While it may be supposed that water temperature is lower during

rainy periods, and this could account for a negative effect of rainfall on calling activity by *Lit. raniformis*, lagged rainfall and water temperature were unrelated in our dataset (Pearson's $r = -0.04$). Saenz *et al.* (2006) hypothesized that acoustic interference from storms or rainfall itself may be the underlying mechanism. We can see two potential mechanisms for *Lit. raniformis*. Firstly, it may be that males of *Lit. raniformis* reduce calling activity following rainfall to reduce acoustic interference with other species in the community, with calling by four species being positively related to lagged rainfall (as above). Secondly, the negative relationship between calling activity and rainfall in *Lit. raniformis* may stem from the sensitivity of this species to rising water levels in lotic situations, where increased flows represent a threat to eggs and weakly swimming early-stage tadpoles. Of the frogs

Table 2. Model-averaged regression coefficients for the six commonly detected species. Variables are as follows: days since September 1 (Days), air or water temperature anomaly (Temp), humidity anomaly (Hum), wind strength (Wind), rainfall anomaly (mm) either for the day of survey (Rain) or for the preceding 7 days (Rain lag). The mean estimates are shown with the 95% CIs in parentheses. Coefficients for the effect of survey effort are not shown.

Species	cos Days	sin Days	Temp	Hum	Wind	Rain	Rain lag
<i>Crinia signifera</i>	2.79 (2.04, 3.61)	-1.18 (-2.06, -0.31)	-0.07 (-0.31, 0.17)	0.00 (-0.34, 0.34)	0.02 (-0.24, 0.30)	0.00 (0.00, 0.00)	1.36 (0.51, 2.36)
<i>Limnodynastes dumerilii</i> ¹	0.26 (-0.47, 1.01)	2.57 (1.06, 4.21)	1.28 (0.44, 2.21)	-0.42 (-1.03, 0.17)	-0.01 (-0.20, 0.18)	0.05 (0.00, 0.12)	1.32 (0.44, 2.30)
<i>Limnodynastes tasmaniensis</i>	1.06 (0.43, 1.71)	0.37 (-0.48, 1.22)	-0.04 (-0.28, 0.20)	-0.29 (-0.77, 0.17)	0.01 (-0.23, 0.24)	0.05 (-0.07, 0.18)	0.62 (-0.01, 1.38)
<i>Litoria ewingii</i> ¹	1.41 (0.65, 2.21)	-1.42 (-2.50, -0.39)	0.16 (-0.14, 0.43)	1.15 (0.39, 1.96)	-0.11 (-0.38, 0.16)	0.00 (-0.03, 0.03)	1.03 (0.20, 1.98)
<i>Litoria raniformis</i>	-0.18 (-0.88, 0.53)	3.47 (2.21, 4.86)	1.18 (0.48, 1.89)	-0.04 (-0.24, 0.16)	-0.10 (-0.33, 0.13)	-0.19 (-0.42, 0.00)	-0.60 (-1.10, -0.11)
<i>Litoria verreauxii</i> ¹	3.07 (1.87, 4.51)	1.27 (-1.20, 4.38)	0.3 (-0.25, 0.86)	1.1 (0.06, 2.22)	-0.06 (-0.45, 0.33)	-0.05 (-0.53, 0.45)	0.13 (-0.47, 0.76)

¹Temp is air temperature for these species.

detected in our study area, *Lit. raniformis* was the most frequently observed in lotic habitats.

In line with Lemckert and Grigg (2010), our data suggest that calling by *Lim. dumerilii* is stimulated by warmer than average air temperatures during the calling season. *Lim. dumerilii* is a terrestrial species that can range up to 1 km from wetlands during the nonbreeding season (Humphries 1979; Anstis 2013). We speculate that the tendency of male *Lim. dumerilii* to call on nights with comparatively warm air temperatures relates to the suitability of such nights for female migration to breeding sites. Finally, the positive relationship between the probability of calling and relative humidity demonstrated here for *Lit. ewingii* and *Lit. verreauxii* may be readily explained by their propensity to call from elevated perches or on land, rather than in the water (Anstis 2013; pers. obs.). Higher relative humidity facilitates hydroregulation in these circumstances (Tracy 1976), allowing prolonged calling.

Other ecological mechanisms could account for the variation in reproductive phenology observed during this study. For example, the focal species may vary in their susceptibility to terrestrial or aquatic predators, and time reproduction to minimize exposure to particular predators (e.g., Lips 2001). Invertebrates and fish are important larval predators for some of the frogs studied here; however, the available evidence suggests that they respond spatially rather than temporally to these predators (Hamer and Parris 2010, 2013). We encourage further research on the reproductive phenology of amphibians and the mechanisms underlying interspecific variation in this trait within communities. As well as insights into niche partitioning and community dynamics, research on reproductive phenology can inform assessments of the effects of anthropogenic disturbances on amphibian communities, including disruptions from climate change (Todd et al. 2011). In particular, we encourage research on the reproductive phenology of amphibians from Australia, Africa, and Eurasia, for which data are scarce.

Acknowledgments

Funding was provided by the Australian Research Council (ARC Centre of Excellence for Environmental Decisions and LP0990161), Australian National Environmental Research Program Hub for Environmental Decisions, Australian Research Centre for Urban Ecology, Victorian Department of Environment, Land, Water and Planning, Growling Grass Frog Trust Fund, Museums Victoria, Melbourne Water and Parks Victoria. GWH was supported by a Victorian Postdoctoral Research Fellowship from the Victorian Department of State Development, Business and Innovation. We thank D. DeAngelis, B. Dobiecki, E.

Sebastian González, A. Hamer, C. Keely, A. Morán Ordóñez, P. Robertson, D. Stokeld, and R. Valentic for their contribution to surveys, along with numerous other colleagues and volunteers. P. Byrne, A. Canzano, B. Casey, L. Conole, C. Crane, D. DeAngelis, K. Ficken, D. Gilmore, P. Grenfell, C. Griffith, A. Hamer, P. Homan, S. Koehler, B. Lane, A. Organ, M. Perry, E. Poole, D. Quinn, C. Renowden, P. Robertson, J. Urlus, M. Venosta, and L. Williams kindly provided access to additional survey data. M. Scroggie suggested the use of a Fourier approach for modeling the seasonality of calling, and two anonymous reviewers provided constructive criticisms on an earlier draft.

Conflict of Interest

None declared.

References

- Aichinger, M. 1987. Annual activity patterns of anurans in a seasonal neotropical environment. *Oecologia* 71:583–592.
- Alford, R. A. 1989a. Competition between larval *Rana palustris* and *Bufo americanus* is not affected by variation in reproductive phenology. *Copeia* 1989:993–1000.
- Alford, R. A. 1989b. Effects of parentage and competitor phenology on the growth of larval *Hyla chrysoscelis*. *Oikos* 54:325–330.
- Alford, R. A. 1999. Tadpole ecology: resource use, competition, and predation. Pp. 240–278 in R. Altig and R. W. McDiarmid, eds. *Biology of anuran larvae*. University of Chicago Press, Chicago, IL.
- Alford, R. A., and H. M. Wilbur. 1985. Priority effects in experimental pond communities: competition between *Bufo* and *Rana*. *Ecology* 66:1097–1105.
- Anstis, M. 2013. *Tadpoles and frogs of Australia*. New Holland, Chatswood.
- Bertoluci, J. 1998. Annual patterns of breeding activity in Atlantic rainforest anurans. *J. Herpetol.* 32:607–611.
- Bertoluci, J., and M. T. Rodrigues. 2002. Seasonal patterns of breeding activity of Atlantic Rainforest anurans at Boracéia, Southeastern Brazil. *Amphib-Reptil.* 23:161–167.
- Brooke, P. N., R. A. Alford, and L. Schwarzkopf. 2000. Environmental and social factors influence chorusing behaviour in a tropical frog: examining various temporal and spatial scales. *Behav. Ecol. Sociobiol.* 49:79–87.
- Bureau of Meteorology 2014. *Climate Data Online*. Commonwealth of Australia, Melbourne, Australia. <http://www.bom.gov.au/climate/data/>
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multi-model inference: a practical information-theoretic approach*, 2nd ed. Springer, New York.
- Canessa, S., and K. M. Parris. 2013. Multi-scale, direct and indirect effects of the urban stream syndrome on amphibian communities in streams. *PLoS One* 8:e70262.
- Canessa, S., G. W. Heard, K. M. Parris, and M. A. McCarthy. 2012. Integrating variability in detection probabilities when designing wildlife surveys: a case study of amphibians from south-eastern Australia. *Biodivers. Conserv.* 21:729–744.
- Chelgren, N. D., D. K. Rosenberg, S. S. Heppell, and A. I. Gitelman. 2006. Carryover aquatic effects on survival of metamorphic frogs during pond emigration. *Ecol. Appl.* 16:250–261.
- Crowley, P. H., and D. M. Johnson. 1982. Habitat and seasonality as niche axes in an odonate community. *Ecology* 63:1064–1077.
- Donnelly, M., and C. Guyer. 1994. Patterns of reproduction and habitat use in an assemblage of Neotropical hyliid frogs. *Oecologia* 98:291–302.
- Dostine, P. L., S. J. Reynolds, A. D. Griffiths, and G. R. Gillespie. 2013. Factors influencing detection probabilities of frogs in the monsoonal tropics of northern Australia: implications for the design of monitoring studies. *Wildl. Res.* 40:393–402.
- Driscoll, D. A. 1998. Counts of calling males as estimates of population size in the endangered frogs *Geocrinia alba* and *G. vitellina*. *J. Herpetol.* 32:475–481.
- Duellman, W. E., and R. A. Pyles. 1983. Acoustic resource partitioning in anuran communities. *Copeia* 1983:639–649.
- Gascon, C. 1992. The effects of reproductive phenology on larval performance traits in a three-species assemblage of central Amazonian tadpoles. *Oikos* 65:307–313.
- Gillespie, G. 2001. *Ecology of the spotted tree frog (Litoria spenceri): an investigation of causes of population decline*. PhD thesis. University of Melbourne, Melbourne.
- Gottsberger, B., and E. Gruber. 2004. Temporal partitioning of reproductive activity in a neotropical anuran community. *J. Trop. Ecol.* 20:271–280.
- Hamer, A. J., and K. M. Parris. 2010. Local and landscape determinants of amphibian communities in urban ponds. *Ecol. Appl.* 21:378–390.
- Hamer, A. J., and K. M. Parris. 2013. Predation modifies larval amphibian communities in urban wetlands. *Wetlands* 33:641–652.
- Hauselberger, K. F., and R. A. Alford. 2005. Effects of season and weather on calling in the Australian microhylid frogs *Austrochaperina robusta* and *Cophixalus ornatus*. *Herpetologica* 61:349–363.
- Heard, G. W., P. Robertson, and M. P. Scroggie. 2008. Microhabitat preferences of the endangered Growling Grass Frog (*Litoria raniformis*) in southern Victoria, Australia. *Aust. Zool.* 34:414–425.
- Heard, G. W., M. P. Scroggie, and B. S. Malone. 2012a. Classical metapopulation theory as a useful paradigm for the conservation of an endangered amphibian. *Biol. Conserv.* 148:156–166.
- Heard, G. W., M. P. Scroggie, and B. S. Malone. 2012b. The life history and decline of the threatened Australian frog, *Litoria raniformis*. *Austral Ecol.* 37:276–284.

- Heard, G. W., M. A. McCarthy, M. P. Scroggie, J. B. Baumgartner, and K. M. Parris. 2013. A Bayesian model of metapopulation viability, with application to an endangered amphibian. *Divers. Distrib.* 19:555–566.
- Heard, G. W., C. D. Thomas, J. A. Hodgson, M. P. Scroggie, D. S. L. Ramsey, and N. Clemann. 2015. Refugia and connectivity sustain amphibian metapopulations afflicted by disease. *Ecol. Lett.* 18:853–863.
- Hollis, G. J. 2003. Ecology and conservation biology of the Baw Baw frog *Philoria frosti* (Anura: Myobatrachidae): distribution, abundance, autoecology and demography. PhD thesis. University of Melbourne, Melbourne.
- Humphries, R. B. 1979. Dynamics of a breeding frog community. PhD thesis. Australian National University, Canberra.
- Hurd, L. E., and R. M. Eisenberg. 1989. Temporal distribution of hatching times in three sympatric mantids (Mantodea: Mantidae) with implications for niche separation and coexistence. *Proc. Entomol. Soc. Wash.* 91:55–58.
- Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harb. Symp. Quant. Biol.* 22:415–427.
- Kronfeld-Schor, N., and T. Dayan. 2003. Partitioning of time as a ecological resource. *Annu. Rev. Ecol. Evol. Syst.* 34:153–181.
- Lawler, S. P., and P. J. Morin. 1993. Temporal overlap, competition, and priority effects in larval anurans. *Ecology* 74:174–182.
- Lemckert, F. L. 2001. The influence of micrometeorological factors on the calling activity of the frog *Crinia signifera* (Anura: Myobatrachidae). *Aust. Zool.* 31:625–631.
- Lemckert, F., and G. Grigg. 2010. Living in the 80s - seasonality and phenology of frog calling activity at Darkes Forest from 1987–1989. *Aust. Zool.* 35:245–250.
- Lemckert, F. L., and M. Mahony. 2008. Core calling periods of the frogs of temperate New South Wales, Australia. *Herpetol. Conserv. Biol.* 3:71–76.
- Lemckert, F. L., T. D. Penman, and M. Mahony. 2013. Relationship of calling intensity to micrometeorology in pond breeding frogs from central eastern New South Wales. *Proc. Int. Acad. Ecol. Environ. Sci.* 3:170–180.
- Lips, K. R. 2001. Reproductive trade-offs and bet-hedging in *Hyla calypsa*, a Neotropical treefrog. *Oecologia* 128:509–518.
- Littlejohn, M. J. 1977. Long-range acoustic communication in Anurans: an integrated and evolutionary approach. Pp. 263–294 in D. Taylor and S. Guttman, eds. *The reproductive biology of amphibians*. Plenum Press, New York.
- Littlejohn, M. J., and A. A. Martin. 1969. Acoustic interaction between two species of Leptodactylid frogs. *Anim. Behav.* 17:785–791.
- Loftus-Hills, J. 1973. Comparative aspects of auditory function in Australian anurans. *Aust. J. Zool.* 21:353–367.
- MacNally, R. C. 1979. Social organisation and interspecific interactions in two sympatric species of *Ranidella* (Anura). *Oecologia* 42:293–306.
- MacNally, R. C. 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.
- Morrison, C. F. 2001. Altitudinal variation in the life history of anurans in southeast Queensland. PhD thesis. Griffith University, Southport.
- Oseen, K., and R. Wassersug. 2002. Environmental factors influencing calling in sympatric anurans. *Oecologia* 133:616–625.
- Parris, K. M. 2002. More bang for your buck: the effect of caller position, habitat and chorus noise on the efficiency of calling in the spring peeper. *Ecol. Model.* 156:213–224.
- Parris, K. M., M. Velik-Lord, and J. M. A. North. 2009. Frogs call at higher pitch in traffic noise. *Ecol. Soc.* 14:25. [online] URL: <http://www.ecologyandsociety.org/vol14/iss21/art25/>.
- R Development Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.r-project.org/>
- Saenz, D., L. A. Fitzgerald, K. A. Baum, R. N. Conner, and D. Adams. 2006. Abiotic correlates of anuran calling phenology: the importance of rain, temperature, and season. *Herpetol. Monogr.* 20:64–82.
- Schwartz, J., and K. Wells. 1984. Interspecific acoustic interactions of the neotropical treefrog *Hyla ebraccata*. *Behav. Ecol. Sociobiol.* 14:211–224.
- Silvertown, J. 2004. Plant coexistence and the niche. *Trends Ecol. Evol.* 19:605–611.
- Smith, M. J., W. Osborne, D. Hunter, and M. E. Douglas. 2003. Geographic variation in the advertisement call structure of *Litoria verreauxii* (Anura: Hylidae). *Copeia* 2003:750–758.
- Smith, K. L., P. M. Oliver, and M. J. Littlejohn. 2012. Morphological and acoustic evidence for hybridisation between two broadly sympatric south-eastern Australian tree frogs *Litoria ewingii* and *L. verreauxii* (Anura: Hylidae). *Aust. J. Zool.* 60:37–45.
- de Solla, S., K. Fernie, G. Barrett, and C. Bishop. 2006. Population trends and calling phenology of anuran populations surveyed in Ontario estimated using acoustic surveys. *Biodivers. Conserv.* 15:3481–3497.
- Spiegelhalter, D. J., N. G. Best, B. P. Carlin, and A. Van Der Linde. 2002. Bayesian measures of model complexity and fit. *J. R. Stat. Soc. Series B Stat. Methodol.* 64:583–639.
- Steelman, C. K., and M. E. Dorcas. 2010. Anuran calling survey optimization: developing and testing predictive models of anuran calling activity. *J. Herpetol.* 44:61–68.
- Thomas, A., B. O'Hara, U. Ligges, and S. Sturtz. 2006. Making BUGS open. *R. News* 6:12–17.
- Todd, B. D., D. E. Scott, J. H. K. Pechmann, and J. W. Gibbons. 2011. Climate change correlates with rapid delays and advancements in reproductive timing in an amphibian community. *Proc. R. Soc. B Biol. Sci.* 278:2191–2197.

- Townsend, C. R., M. Begon, and J. L. Harper. 2008. *Essentials of ecology*, 3rd ed. Blackwell Publishing, Oxford, UK.
- Tracy, C. R. 1976. A model of the dynamic exchanges of water and energy between a terrestrial amphibian and its environment. *Ecol. Monogr.* 46:293–326.
- Wagner, W. E. Jr. 1992. Deceptive or honest signalling of fighting ability? A test of alternative hypotheses for the function of changes in call dominant frequency by male cricket frogs. *Anim. Behav.* 44(Part 3):449–462.
- Watson, G. F., M. J. Littlejohn, D. F. Gartside, and J. J. Loftus-Hills. 1985. The *Litoria ewingi* complex (Anura: Hylidae) in South Australia VIII. Hybridization between *L. ewingi* and *L. verreauxi alpina* in the Mount Baw Baw area, South Central Victoria. *Aust. J. Zool.* 33:143–152.
- Welch, A. M., R. D. Semlitsch, and H. C. Gerhardt. 1998. Call duration as an indicator of genetic quality in male Gray Tree Frogs. *Science* 280:1928–1930.
- Wells, K. D. 2007. *The ecology and behavior of amphibians*. University of Chicago Press, Chicago, IL.
- Wilbur, H. M., and R. A. Alford. 1985. Priority effects in experimental pond communities: responses of *Hyla* to *Bufo* and *Rana*. *Ecology* 66:1106–1114.
- Williamson, I., and C. M. Bull. 1992. Life history variation in a population of the Australian frog *Ranidella signifera*: time of egg laying. *J. Herpetol.* 26:322–327.
- Wong, B. B. M., A. N. N. Cowling, R. B. Cunningham, and C. F. Donnelly. 2004. Do temperature and social environment interact to affect call rate in frogs (*Crinia signifera*)? *Austral Ecol.* 29:209–214.