Do temperature and social environment interact to affect call rate in frogs (*Crinia signifera*)?

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Abstract Acoustic displays are pervasive and conspicuous forms of sexual advertisement used by animals to attract mates. Evidence suggests that individuals may use environmental cues and/or the presence of other displaying animals to select the best times for display to optimize the chances of mating. Less well-known is how the physical and social environment might interact to affect the actual content of the display itself. We examined the effects of social environment and temperature on calling rate in a frog *Crinia signifera*. We found that both variables interacted to affect call rate but only among continuous callers. Call rate increased with temperature in individuals calling continuously on their own but no relationship was found in frogs calling continuously in the presence of others, either in a duet or in a group calling situation. We suggest that the temperature sensitivity of calling rate in frogs could depend on the social environment of the caller. As such, we suggest caution in generalizing about the way temperature affects calling rates in frogs and encourage greater consideration of how physical and social environments might interact to influence the signal content of acoustic displays.

Key words: male–male competition, Myobatrachidae, social environment, temperature.

INTRODUCTION

Many animals signal acoustically for the purpose of attracting mates. However, acoustic displays can be costly, involving expenditure of time and energy (Mac Nally 1981; Lemckert & Shine 1993; Prestwich 1994; Judge & Brooks 2001), and exposing individuals to a heightened risk of predation (reviewed in Kotiaho 2001). Evidence suggests that individuals may use environmental cues and/or the presence of other displaying animals to select the best times for display (Brooke *et al.* 2000). In this way, individuals may maximize the probability of mating while minimizing associated costs. However, environmental and social factors might affect not only the timing of acoustic displays, but also the actual content of the signal itself.

The temporal and spectral properties of acoustic signals often play a pivotal role in conveying important information about the quality of the signaller to other individuals (Gerhardt 1988). In many species, it is common for displaying animals to interact and mutually adjust the content of their signals in response to one another (Wells 1988). In many arthropods and anurans, for example, fine-scale adjustments made to the temporal components of the call allow neighbouring individuals to avoid complete signal overlap during vocal interactions (Greenfield 1994). Individuals may also vary their signalling effort and alter the actual number of calls produced per unit time. Specifically, males may be selected to match or exceed the signalling output of their neighbours to remain attractive to prospective mates, particularly if high signalling effort correlates with attractiveness (Ryan 1988). Male frogs, for instance, often elevate their call rate when chorus densities are high and when acoustic competition is at its most intense (reviewed in Wagner 1989).

Acoustically displaying ectothermic animals face an additional challenge as body temperature directly influences the physiological reaction rates that power the muscles involved in sound production (Prestwich 1994; Navas & Bevier 2001). Because body temperature is often dependent on environmental temperature, changes in the thermal environment of the caller can lead to conspicuous temperature-dependent changes in call structure. For example, numerous studies have shown a positive correlation between temperature and rate of calling in both insects and frogs (for review, see Prestwich 1994).

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The effects of social environment and temperature on signal content have often been considered in isolation. Very few studies have explicitly investigated the possibility that these variables might interact to affect call structure. Indeed, as far as we are aware, evidence for an interaction exists only anecdotally from a North American study on calling rate in spring peepers, *Pseudacris crucifer* (Wells *et al.* 1996). In that study, call rate was found to increase with temperature in a manner consistent with other species of frogs. However, it was observed that this temperature relationship was 'modified' in animals that were alternating their calls. We set out to examine the possibility that such interactions between temperature and social environment could be present and could influence call rate in natural populations of the Australian frog *Crinia signifera* Girard.

METHODS

The common eastern froglet (*C. signifera*) is a small terrestrial frog found across temperate regions of south-eastern Australia. The advertisement call of *C. signifera* is a short, rapidly repeated series of pulses with a dominant frequency of approximately 3 kHz. Males may call continuously in bouts lasting up to 5 min (Littlejohn 1959), with some individuals attaining a call rate of up to 167 calls min^{-1} (B. B. M. Wong, unpubl. data). Populations typically breed over winter, although there are considerable interpopulational and year-to-year differences in the timing and duration of the breeding season (Lemckert 2001).

We recorded and analysed frog calls at three sites in Canberra (35°17′S, 149°08′E) from 9 May to 16 August 1999. The three sites were close to each other but occurred in separate drainage lines. Frogs called from the base of grasses, sedges and rushes in ephemeral pools along drainage ditches.

Crinia signifera are difficult to locate without disturbing their behaviour. Furthermore, they are small animals (snout-vent length ± standard error (SE) = 2.10 ± 0.06 cm; body mass ± SE = 1.00 ± 0.05 g), making reliable measurements of body temperature difficult (Navas & Bevier 2001). However, with proper consideration of microhabitat selection (Navas 1996), local microsite temperature is a reliable proxy for body temperature in small frogs (Navas 1996; Navas & Bevier 2001). Because the frogs called in areas that were saturated or inundated with water (Straughan & Main 1966; pers. obs.), we chose water temperature near the caller to best represent both the body temperature of the caller and the thermal environment of the species. Thus, the temperature of the calling environment was measured by immersing the bulb of an alcohol thermometer in shallow water (<5 cm deep) shaded by vegetation near the caller.

Calls were sampled three afternoons every week during the study period (*n* = 42 days). All three sites were sampled sequentially (approximately 20 min site^{-1}) from 15.00 to 17.00 hours (Australian Eastern Standard Time). The narrow time range was chosen to minimize temporal variation in light conditions and to allow us to sample calls over a wide range of temperatures. The daily order of site visitation was randomized to avoid potentially confounding site with sampling time.

We sampled the calls of up to 8 animals from each location and, whenever possible, we recorded a minimum of five calls per male. We recorded calls using a Sony TCD-D10 Pro II digital audio tape recorder and Senheiser MD-400 microphone. We used a Sony PBR-330 parabolic reflector to minimize disturbance to the calling frogs by recording them from <3 m away. An additional 10 min of uninterrupted audio recording taken from each site was used to census the number of callers at the time of the visit.

Recordings of calls from individual frogs were digitized using a Power Macintosh 7100/66 computer with sound card (Video Vision) and analysed using Canary. After filtering out background noise, we measured the following temporal and spectral call parameters: call rate (calls min^{-1}), pulse rate (pulses s^{-1}), call duration (msec), the interval between calls (s), the number of pulses, and peak frequency (kHz).

Field observations and preliminary data analysis revealed that calling frogs could be categorized into two distinct groups based on variance in the interval between calls. Frogs that had a coefficient of variation (CV) for their call interval of >0.15 were classed as 'intermittent callers' and those with CV < 0.15 were classed as 'continuous' (mean CV ± SE: intermittent = 0.439 ± 0.041, continuous = 0.057 ± 0.004). We identified three social environments: calling alone; duetting; and calling in the presence of two or more other callers. Duetting was only observed between pairs of continuously calling males and was characterized by the matching of call frequency peaks between callers (B. B. M. Wong, unpubl. data). We found no evidence of call alternation when more than two frogs were calling. Given these observations, each frog recording was assigned to one of five categories: calling intermittently on its own; calling intermittently in a group; calling continuously on its own; calling continuously in a group; and calling continuously in a duet.

We recorded several males (range 0–8) from each site on each sampling day, which resulted in non-independent readings. Therefore, we used site and day as random effects in Poisson generalized linear mixed models (Schall 1991) when the number of callers was the response variable, and we used site and day as random effects in linear mixed models (Searle *et al.* 1992) when call rate was the response variable. The respective models were fitted using generalized linear

mixed models and restricted maximum likelihood procedures in Genstat (Genstat Committee 1993). Wald tests were used to test the significance of fixed effects. As the number of callers and call rates can respond to seasonally changing factors such as hormone levels (Verrell 1990), we included the term 'date' in the statistical models. To model possible curvature in the seasonal variation in the number of callers flexibly, we used polynomials in date as explanatory variables. To model call rate, we used date, water temperature and social environment as explanatory variables. The analysis of call rate showed that intermittent and continuous callers formed separate populations and so separate analyses are given for these groups.
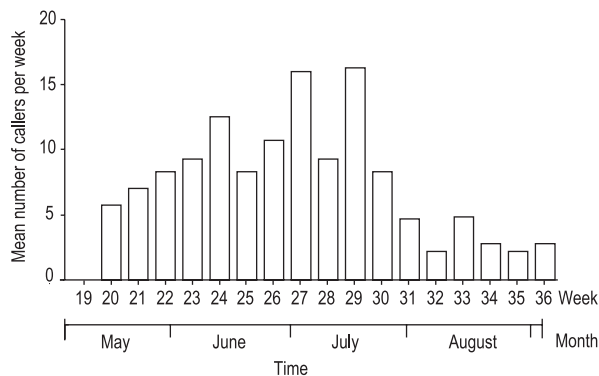

Fig. 1. Mean number of frogs recorded calling per week during the study.

RESULTS

We made 212 individual call recordings over the 42 days of sampling carried out during the study period. Call rate in *C. signifera* correlated positively with pulse rate and negatively with pulse number, intercall interval, call duration and dominant frequency (Table 1).

The number of calling individuals observed over the course of the study varied with date. The quadratic term in date was highly significant ($\chi^2 = 23.24$, degrees of freedom (d.f.) = 1, $P < 0.001$) showing strong curvature through the study period. Specifically, caller number reached a peak in winter before decreasing with the approach of spring (Fig. 1).

In the analysis of call rate for continuous callers, after adjustment for date and site, we found a significant interaction between water temperature and social environment ($\chi^2 = 11.7$, d.f. = 2, $P = 0.003$; Fig. 2) although neither main effect was significant. That is, the relationship between call rate and temperature was significantly different for different social environments. Call rate increased significantly with water temperature for males calling alone ($t = 2.99$, d.f. = 157, $P = 0.003$) but water temperature did not affect the calling rates of males calling either in a group or in a duet (Fig. 2; Table 2).

In the analysis of call rate for intermittent callers, we found no significant interaction between water temperature and social environment (Fig. 3; Table 2). However, males calling intermittently in the presence of other callers were found to call at higher rates than

Table 1.   Correlation matrix for the temporal and spectral components of the call ($n = 212$)

	Call rate	Call duration	Intercall interval	Pulse no.	Pulse rate	Frequency
Call rate	–					
Call duration	−0.82★	–				
Intercall interval	−0.81★	0.77★	–			
Pulse no.	−0.70★	0.86★	0.69★	–		
Pulse rate	0.44★	0.37★	−0.23★	0.06	–	
Frequency	−0.33★	0.39★	0.34★	0.38★	−0.09	–

★$P < 0.01$.

Table 2.   Inferences concerning slopes of lines relating call rate to water temperature in different social environments

	Slope	SE	t	P
Continuous (d.f. = 157)				
Single	8.92	2.99	2.99	0.003
Duet	0.34	2.66	0.13	0.897
Group	−4.71	3.00	−1.57	0.118
Intermittent (d.f. = 31)				
Single	−0.44	1.39	−0.32	0.751
Group	−0.77	1.80	−0.43	0.670

d.f., degrees of freedom; SE, standard error; t, t-test value.

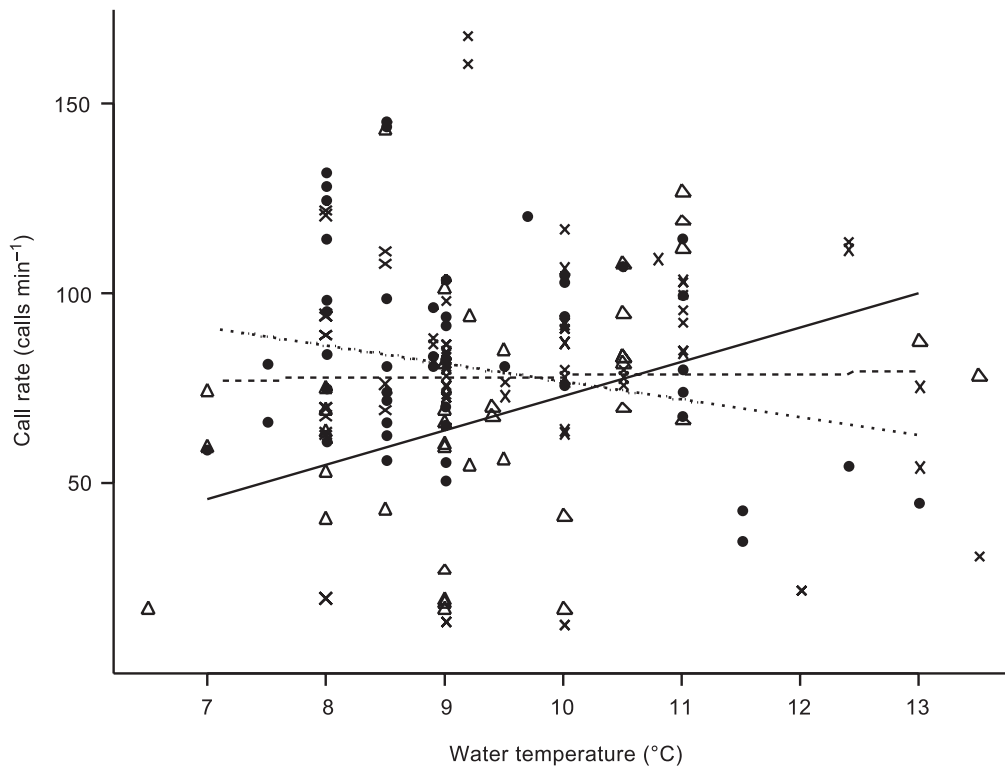**Fig. 2.**   Relationship between temperature and calling rate in continuous callers. (−△−), solitary, $n = 42$; (--✕--), duet, $n = 74$; (···●···), group, $n = 54$.
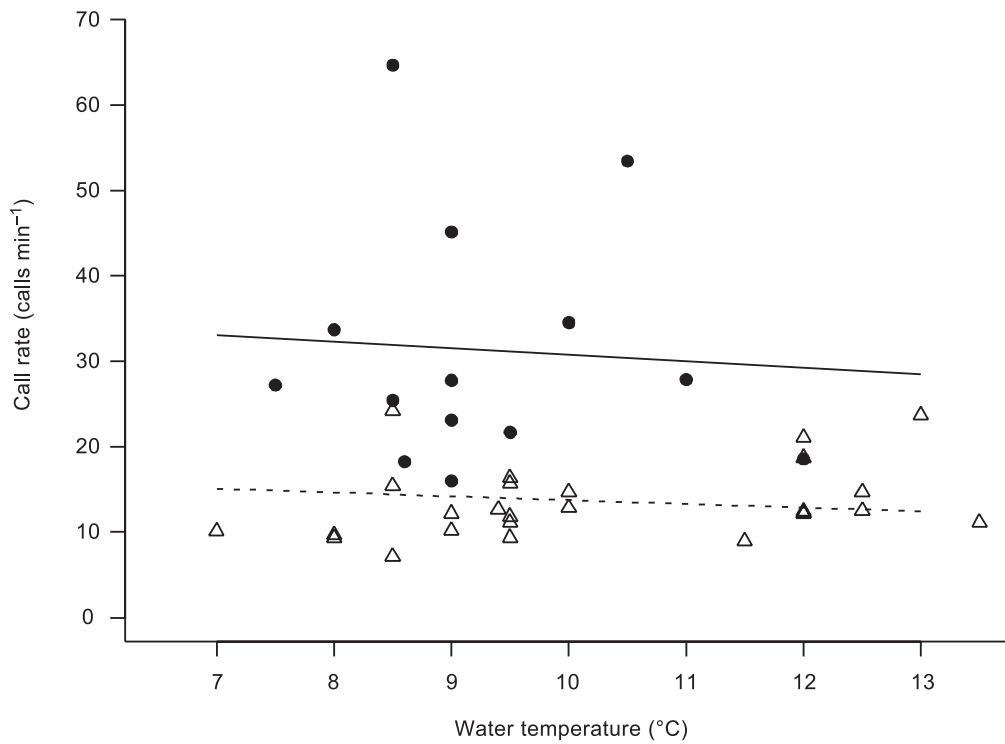

Fig. 3.   Relationship between temperature and calling rate in intermittent callers. (--△--), solitary, $n = 28$; (−●−), group, $n = 14$.

males calling intermittently on their own ($\chi^2 = 45.41$, d.f. = 1, $P < 0.001$; Fig. 3).

DISCUSSION

Interactions between the social and physical environment can have a profound impact on calling in frogs. For example, in the terrestrially breeding frog *Cophixalus ornatus*, Brooke *et al.* (2000) showed that such interactions may be important as a trigger in chorus initiation. However, in addition to their roles in influencing the timing and onset of chorusing activity, a possible interaction between temperature and social environment may have important consequences for the content of acoustic displays as manifested in the calling rate of *Crinia signifera* in the present study.

Among continuously calling males, we found that changes in call rate with temperature depended on the social environment of the caller. It is generally assumed that call rate in frogs increases with temperature (Prestwich 1994). Our study suggests that this is not necessarily the case. A positive correlation between temperature and call rate was found only in individuals that were calling continuously on their own. The effect of water temperature on call rate was not significant for animals calling in a duet or group.

It appears that the presence of other frogs can alter the normally positive relationships between temperature and call rates. This has previously only been suggested anecdotally for duetting animals. In spring peepers (*Pseudacris crucifer*), call rate was shown to be highly temperature dependent, but this thermal dependence was modified by call alternation between neighbouring males (Wells *et al.* 1996). In that study, however, no information was given as to how calls were actually modified. In quacking frogs (*Crinia georgiana*), Gerhardt *et al.* (2000) suggested that call matching between duetters probably allows males to make themselves as attractive to females as those of their nearest rivals without expending energy unnecessarily. If this is the case, duetting individuals might not need to attain the level of calling effort necessary for temperature effects to manifest.

Apart from anecdotal evidence from work done on duetting frogs, we are unaware of any other studies that have shown that the temperature sensitivity of call rate may be affected by social environment. Studies often report a strong positive relationship between call rate and competition (Wagner 1989). Given that temperature has often been reported to have a similar positive effect on call rate (Prestwich 1994), it is apparent that the two processes could often be confounded. In the present study, we recorded a strong seasonal pattern of variation in the number of callers, which increased in late autumn and reached its peak in winter, before decreasing again with the approach of spring. This finding is consistent with previous studies, suggesting a peak in calling activity centred around winter (reviewed in Lemckert 2001). However, in the present study, we adjusted for date in our models to take into account this temporal variation in the number of callers. Having controlled for seasonal effects, frogs calling in groups were shown to have different sensitivities of call rate from those calling alone. It seems reasonable to suppose that this difference could be caused by competition or by some other effect of group calling such as an effort to increase the attractiveness of the group itself (R. A. Alford, pers. comm.). These possibilities warrant further investigation through, for example, playback and/or phonotaxis experiments.

Whether a male called continuously or intermittently also had a bearing on the effect of temperature on call rates. There was no effect of temperature on call rate for intermittent callers. In general, males making only a small investment in calling might be less sensitive to temperature because they are not calling close to their physiological limits. This pattern can be seen both within and across species. The differences in thermal sensitivity between continuous and intermittent callers in *C. signifera* are consistent with the findings of Navas (1996). He studied the thermal dependency of call rates in high elevation anurans and found that higher temperatures only elevated calling rates in species that called vigorously.

Our results place an important caveat on generalizing about the way temperature affects acoustic signals in frogs. Ectotherms do not always perform at levels close to their maximum physiological limits where temperature effects may manifest (Hertz *et al.* 1988). Males do not always display at maximum intensities to attract mates (Patricelli *et al.* 2002). Given the high energetic demands of calling (Mac Nally 1981; Lemckert & Shine 1993; Prestwich 1994; Judge & Brooks 2001), male anurans ought to remain responsive to changes in their environment so as to signal at levels that would maximize their chances of reproductive success without expending unnecessary energy (Gerhardt *et al.* 2000). Our results, and those reported by Navas (1996), indicate that temperature effects on call rate could depend on the calling effort of the individual and also on the social environment of the caller. We suggest that future studies should give greater consideration to how different factors might interact to affect signal content in acoustically displaying animals.

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