



Adaptive plasticity in calling site selection in grey treefrogs (*Hyla versicolor*)

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Accepted 6 December 2013; published online 17 January 2014

Abstract

Calling behaviour is an essential component of gaining access to mates, and calling site selection may be an important component of effective communication. Environmental factors like microclimate, or the presence of competitors and predators often show seasonal or spatial variation, and behavioural plasticity that allows the caller to adjust to this variation may be adaptive. Prompted by the observation of across-season variation in elevated calling site use in our grey treefrog population, we formulated three hypotheses about their calling site choice and tested them using field observations and behavioural trials in the lab. We found that calling site selection is largely determined by local temperature regimes, and suggest that this temperature-based plasticity in calling site selection is adaptive because it allows males to increase their metabolic efficiency and mate attraction effectiveness. The mere presence of heterospecific competitors and predators did not affect calling site selection at the pond, but close proximity to a predator during behavioural trials did reduce calling activity. This suggests that grey treefrog males attend to the presence of predators, that they can assess the degree of risk associated with predator proximity, and that they can adjust calling behaviour adaptively to reduce the chances of being detected by a predator.

Keywords

acoustic competition, predator avoidance, temperature preference, calling behaviour.

1. Introduction

Calling site preferences may be an important component of effective communication, because the resulting call site segregation in either horizontal or vertical space should reduce the negative effects of acoustic interference (i.e., Hödl, 1977; Luther, 2009), and strengthen reproductive isolation by physically separating members of different species displaying within multi-

species assemblages (Ptacek, 1992; Höbel & Gerhardt, 2003). It is therefore not surprising that calling site preferences have been reported for many acoustically communicating animals, including insects (Claridge et al., 1979; Diwakar & Balakrishnan, 2007; Schmidt et al., 2013), frogs (Hödl, 1977; Drewry & Rand, 1983; Etges, 1987) and birds (Luther, 2009).

While acoustic interference from conspecific or heterospecific competitors is certainly an important selective force influencing calling site selection — and the one that has received most interest so far —, it is not the only one. Calling behaviour, which is an essential component of gaining access to mates in many acoustically communicating animals, also exposes the caller to predators and parasites (reviewed in Zuk & Kolluru, 1998). Many animals have the ability to assess predation risk and respond behaviourally to variation in risk (see Lima & Bednekoff, 1999, and references therein), and consequently calling site selection might also be affected by the vertical and horizontal distribution of predators and parasites.

In addition to the presence of competitors and predators, calling site selection may further be influenced by abiotic factors. Local temperature regimes may be particularly important for ectothermic animals such as insects and anurans, and not surprisingly, ectotherms usually show thermal preferences (Angilletta et al., 2002). For example, ambient temperature is an important factor influencing whether males of a given anuran species do or do not call (e.g., Hauselberger & Alford, 2005; Hsu et al., 2006), and various call characters change in predictable fashion with male body temperature (McLister, 2001; Gerhardt & Huber, 2002). Although anuran body temperatures often mirror the thermal environment in which they live (Fouquette, 1980; Navas & Araújo, 2000), some species are capable of behavioural thermoregulation, and achieve reduced thermal variance compared to the range of temperatures encountered in their environment (Sinsch, 1984; Navas, 1996).

Calling site preferences show a certain degree of species-specificity, but many species also show plasticity in calling site selection (Ptacek, 1992; Höbel & Gerhardt, 2003). This is not surprising, since behavioural plasticity would allow animals to adjust to seasonal or spatial variation in the environment that may otherwise limit the expression of species-specific preferences. We became interested in the factors that affect calling site selection after observing seasonal variation in the perches grey treefrogs (*Hyla versicolor*) use in our study population in Wisconsin. Early in the breeding season, males fre-

quently call from aquatic sites, often partly submerged in water, but switch to almost exclusive use of elevated calling sites later in the season. Elevated sites (trees in and around the pond) are available throughout the entire breeding season, suggesting that this seasonal variation in calling site use was not simply a function of a lack of suitable elevated options, but resulted from changes in behavioural preferences.

A survey of the abiotic (temperature) and biotic (presence of calling heterospecifics or predators) factors at the study pond across the grey treefrog breeding season suggested that both the presence of calling heterospecifics (spring peeper, *Pseudacris crucifer*) and the presence of predatory aquatic frogs (green frogs/bullfrogs, *Lithobates clamitans/L. catesbeiana*) varied across the season. Early in the season, spring peepers which call predominantly from lower-elevation perches, were very common while the prevalence of predatory aquatic frogs increased towards the latter part of the grey treefrog breeding season. There was also a change in temperature, with higher water than air temperatures during the early part of the season, and higher air than water temperatures during the latter part.

These observations prompted us to formulate three hypotheses that addressed the causes of plasticity in calling site selection of grey treefrogs in our study site: (i) the warmer temperature hypothesis: this hypothesis posits that males prefer warmer calling sites, and makes the prediction that males will call from terrestrial sites if the air temperature is above water temperature, and vice versa. (ii) The predator avoidance hypotheses: this hypothesis posits that males avoid calling sites at which they are vulnerable to predators, and makes the prediction that grey treefrog males use elevated calling sites to vertically distance themselves from the larger and predominantly aquatic bullfrogs and green frogs. (iii) The heterospecific interference hypothesis: this hypothesis posits that males avoid calling sites where they are faced with acoustic competition, and makes the prediction that grey treefrog males use elevated calling sites to minimize acoustic interference from spring peepers, which at our study site call predominantly near water level. We conducted field observations to test all three hypotheses. In addition, we conducted behavioural trials in the lab, in which we manipulated air and water temperature of potential calling sites, as well as the presence/absence of a predator, in order to test the warmer temperature hypothesis and the predator avoidance hypothesis.

2. Material and methods

2.1. Field observations

Field observation of calling site selection of grey treefrogs (*Hyla versicolor*) males took place from May to July 2011 at Byer's pond, adjacent to the University of Wisconsin–Milwaukee (UWM) Field Station, Saukville, WI, USA. The pond is 1.077 ha large, and is home to sizeable populations of spring peepers (*Pseudacris crucifer*), grey treefrogs (*H. versicolor*), green frogs (*Lithobates clamitans*), and a smaller population of bullfrogs (*L. catesbeiana*). Other species of anurans also breed at the pond (*Bufo americanus*, *L. sylvatica*, *L. pipiens*), but their breeding season did not overlap with that of grey treefrogs.

On 8 nights between May 20–June 26 (every 5 ± 3 nights) we sampled the pond for calling grey treefrog males ($N = 127$ males). For every male we took the following measurements: (i) calling site characteristics: terrestrial (coded as 100% in air) or in water (coded as 0–75% in air, in steps of 25%, depending on how much of the frog's body was submerged); (ii) air–water temperature gradient, by measuring air temperature and water temperature adjacent to male (measured with Miller & Weber quick read thermometer); (iii) the body temperature of the male (measured with an Extech 42511 IR thermometer pointed towards the top of the male's head); (iv) presence of predatory frogs; and (v) presence of acoustic competitors. We used visual and auditory sampling during the nightly pond visits to look for the presence of bullfrogs, green frogs, and spring peepers, and documentation anywhere in the pond resulted in a positive score for predator/competitor presence. In addition, we stationed two automatic recorders (Song Meter, Wildlife Acoustics) at the pond, which recorded from 25 April–1 August 2011 (for 5 min every hour, for a total of 125 min per day). We used these recordings to verify that our visual/auditory sampling had not overlooked the presence of these species.

2.2. Calling site choice experiments

We constructed cylindrical calling site choice arenas, 50 cm in diameter and 100 cm high. Each arena consisted of a cylindrical plastic container as the base (50 cm diameter, 25 cm high), and hardware cloth mesh as the sides and top. Arenas were filled 15 cm deep with pond water, and

contained one upright branch, thus providing both aquatic and terrestrial perch options.

Arenas were set up in groups of four inside a climate-controlled room at UWM. Air temperature was manipulated via the room's thermostat. Water temperature was manipulated with aquarium heaters (to increase water temperature) or ice cubes (to decrease temperature) prior to the start of the experiments. Target air and water temperatures were constant within $\pm 1^\circ\text{C}$. Because 20°C is the across-season average temperature at which grey tree frogs are calling (pers. obs.; see also Results section), we gave males the choice to settle at this temperature, or at a lower water or air temperature (15°C vs. 20°C), and at this and at a higher water or air temperature (20°C vs. 25°C). We also conducted control trials in which both water and air temperatures were the same (20°C).

To test the effects of temperature and predator presence on calling site choice we conducted a series of trials in which we manipulated the temperature of potential calling sites (water and air temperature), as well as the absence/presence of a predator (live green frog). While both green frogs and bullfrogs prey on grey treefrogs, bullfrogs are a larger and more effective predator on other anurans (Hamilton, 1948; Stewart & Sandison, 1972; Werner et al., 1995; Schwartz et al., 2000). Nevertheless, we opted to use live green frogs as our model predator because they are more common at our study site, and thus local grey treefrogs should have more experience with them. Also, we did not want to risk losing one of our test treefrogs to actual predation during the trials, which would have been more likely when using a bullfrog. During trials testing the effect of temperature on calling site choice, only one focal male grey treefrog was placed inside each arena. During trials testing the effect of the presence of a predator on calling site choice, each arena contained one focal male grey treefrog and one green frog (no predation attempts took place during the trials and all test frogs were released unharmed at the end of the experiment).

During each trial we scored whether the focal male (i) settled in the water, (ii) used a terrestrial perch anywhere in the arena (either on the branch, container rim or hardware cloth of the arena wall) and (iii) started to call. Trial duration was 30 min, after which calling site choice and calling activity were scored. We tested 6–12 males in each temperature gradient/predator presence treatment, for a total of 72 tested frogs. Experiments took place during the middle part of the grey treefrog breeding season.

2.3. *Statistical analysis*

To test whether male body temperature varied across observation nights, we used ANOVA. To test which factors affected variation in male body temperature, we used a general linear model with observation date, air temperature and water temperature entered as factors in the model.

To test which factors affected variation in male calling site selection in nature, we used a general linear model with air temperature, water temperature, their interaction, the presence of calling heterospecifics, and the presence of predators entered as factors in the model.

To test which factors affected male perch selection and calling activity during choice trials, we used logistic regressions, with temperature gradient, predator absence/presence, and their interaction, entered as factors in the model. During the choice experiments male treefrogs were given a choice of air and water temperatures differing by 5°C, either in a low range (15°C vs. 20°C) or a high range (20°C vs. 25°C). Since the analysis revealed that the absolute temperatures did not affect the frog behaviour, but the direction of the thermal gradient did (see Figure 4c, d), we lumped the data from the low and high test ranges and transformed the absolute temperature values to thermal gradients. Here -5 indicates that the air temperature in a given trial was 5°C lower than the water temperature, and $+5$ indicates that the air temperature was 5°C higher than the water temperature. All statistical tests were implemented in JMP 8.0.2.

3. Results

3.1. *Field observations*

The proportion of males found in elevated sites varied from 0–86% between sampling nights (Figure 1). Calling site choice in nature was affected by an interaction between air and water temperature, but not by absolute values of air or water temperature, or the presence of calling heterospecifics or predators (see Table 1).

Air temperature during the study period ranged from 8.5–26.6°C, water temperature ranged from 15.8–23°C. Temperature differences between the two media ranged from -7.5°C (i.e., air being 7.5°C colder than water) to 4.3°C (i.e., air being 4.3°C warmer than water) (see Figure 2a, d).

Body temperature of grey treefrog males varied across observation nights; it ranged from 12.9–26.6°C (Figure 2b–d). Calendar date did not affect body

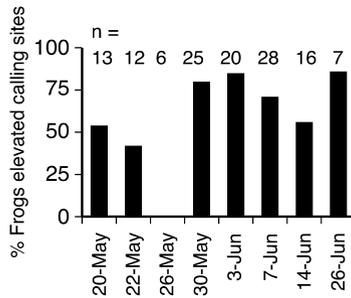


Figure 1. The proportion of grey treefrog males that called from terrestrial perches on each of the 8 observation nights. Note that on May 26, when air temperature was particularly low (see Figure 2d), the few grey treefrog males that did call all chose aquatic calling sites. The numbers on top of the chart denote sample size.

temperature ($F_{1,125} = 0.05$, $p = 0.82$), but both air ($F_{1,125} = 84.05$, $p < 0.0001$) and water temperature ($F_{1,125} = 9.17$, $p = 0.003$) did. This suggests that grey treefrog males do not try to obtain a fixed body temperature by choosing calling sites in water or on land. Rather, their body temperature reflects the temperature of the medium they call from, which they choose based on the local temperature gradient seeking out the warmer medium.

The breeding season of grey treefrogs overlapped with those of spring peepers and with the presence of green frogs and bullfrogs (Figure 3). We detected the first evidence of the presence of green frogs and bullfrogs (visual and/or auditory) during our on-site surveys on June 1st. Long-term recorder data confirmed this assessment. The presence of calling heterospecifics or predators (see Table 1) did not affect calling site selection in nature, though.

Table 1.

Effects of air and water temperature, their interaction, and presence of calling heterospecifics (spring peeper) and predators (bullfrogs/green frogs) on calling site selection of grey treefrogs at the study pond.

| Variable | df | <i>F</i> | <i>p</i> |
|-------------------------------------|--------|----------|----------|
| Air temperature | 1, 125 | 0.057 | 0.81 |
| Water temperature | 1, 125 | 1.053 | 0.31 |
| Air temperature × Water temperature | 1, 125 | 12.947 | 0.0005 |
| Heterospecifics | 1, 125 | 0.145 | 0.70 |
| Predator | 1, 125 | 0.929 | 0.34 |

Only the interaction between air and water temperature significantly affected calling site selection.

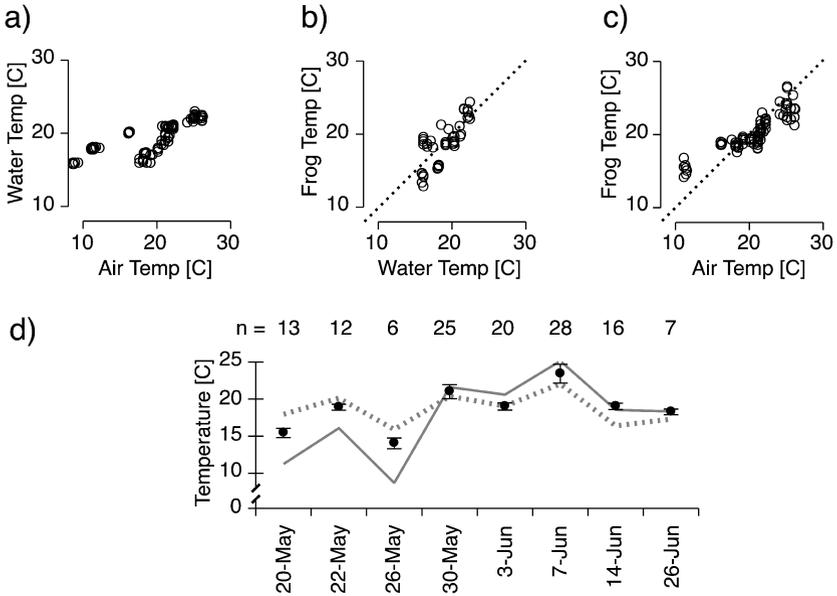


Figure 2. Ambient air and water temperature, and their relation with frog body temperature during the study period. (a) Relationship between air and water temperature at locations frogs were observed calling. (b) Relationship between water temperature and frog body temperature in the cases where frogs were found calling in water. (c) Relationship between air temperature and frog body temperature in the cases frogs were found calling on terrestrial perches. (d) Body temperature (mean \pm SD) of calling grey treefrog males on 8 observation nights, shown relative to the associated air (solid line) and water temperatures (dashed line). The numbers on top of the chart denote sample size. Note that early in the breeding season night-time air temperature was much lower than water temperature, while later in the season air temperature tended to be above water temperature.

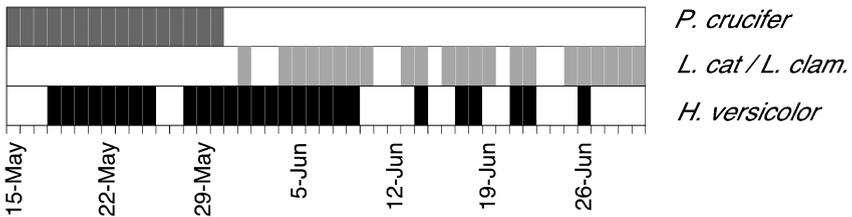


Figure 3. Calling activity of grey treefrogs (*Hyla versicolor*), spring peepers (*Pseudacris crucifer*) and bullfrogs/green frogs (*Lithobates catesbeiana*/*L. clamitans*) during the observation period. Since bullfrogs/green frogs became active at roughly the same time, and both prey on grey treefrogs, we lumped their activity data for this figure. Data on calling activity were obtained from the long-term recorders stationed at the pond.

3.2. Calling site choice experiments

Grey treefrog males showed a preference for residing in the warmer environment; they chose terrestrial sites in the trials in which the air temperature was higher than the water temperature, and aquatic sites in the trials in which the water temperature was higher than the air temperature (Figure 4a, c; Table 2). When both air and water was the same temperature (20°C), half the frogs settled on land, and half in water (Figure 4c, right).

The presence of a predator did not affect where grey treefrog males settled — males still preferred the warmer environment (Figure 4a, c; Table 2). However, the presence of a predator did affect whether males started to call. While the majority of males in the predator-absent trials did call, only a fraction of the ones in the predator-present trials did (Figure 4b, d; Table 2).

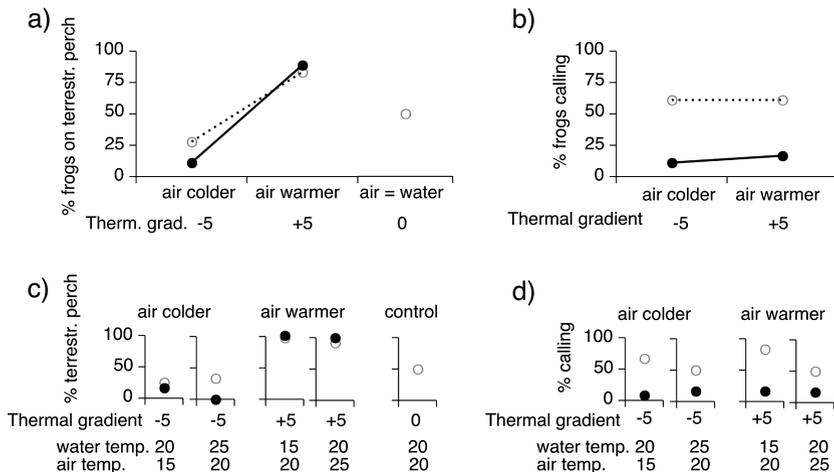


Figure 4. Perch site selection and calling activity of grey treefrogs during perch choice trials. (a) Grey treefrog males did not have a general preference for terrestrial perches, but choose them only when the air was warmer than the water; this choice was similar whether a predator was present (filled symbols) or absent (open symbols); when air and water temperatures were the same, half the frogs choose terrestrial and half choose aquatic perches. (b) The majority of grey treefrog males started to call during the trials in which no predator was present (open symbols), while males largely refrained from calling when a predator was present (filled symbols). (c, d) The general patterns of perch selection (terrestrial when air is warmer than water) and calling activity (more males calling when predator is absent) were not affected by the absolute temperature values at which frogs were tested.

Table 2.

Effects of thermal gradient, predator presence, and their interaction on perch selection and calling activity of grey treefrogs during perch choice trials.

| Behaviour | Variable | df | χ^2 | <i>P</i> |
|-------------------|------------------------------------|-------|----------|----------|
| Terrestrial perch | Thermal gradient | 3, 72 | 55.10 | <0.0001* |
| | Thermal gradient \times Predator | 3, 72 | 0.54 | 0.46 |
| | Predator | 3, 72 | 2.44 | 0.12 |
| Calling | Thermal gradient | 3, 72 | 0.16 | 0.69 |
| | Thermal gradient \times Predator | 3, 72 | 1.42 | 0.23 |
| | Predator | 3, 72 | 18.23 | <0.0001* |

The direction of the thermal gradient was important for whether frogs settled on terrestrial perches, with frogs preferring to settle in the warmer environment. By contrast, the presence of a predator was the main determinant for whether frogs started to call or not.

* Significant difference.

4. Discussion

In grey treefrogs, calling site selection is a plastic response to variation in abiotic and biotic environmental factors, particularly ambient temperature regimes. Males prefer warmer environments, and choose their calling sites accordingly. Early in the breeding season night-time water temperature is frequently above air temperature, resulting in a larger proportion of males calling from aquatic sites. Later in the season temperatures are higher in general, and air and water temperatures are more similar, resulting in most males calling from terrestrial perches. In proximity to potential predators males do not refrain from settling in the preferred (warmer) environment, but they largely refrain from calling, i.e., from engaging in a behaviour that would make them more conspicuous to predators.

Anuran call parameters are frequently temperature dependent, and female frogs often show preferences for traits that increase with higher temperatures (Gerhardt & Huber, 2002). For example, call rate increases with temperature, and higher call rate is almost universally preferred by female frogs (Gerhardt & Huber, 2002). Further, because trunk muscle contraction speed and strength increases with temperature, so does acoustic energy output (McLister et al., 1995), and higher call amplitude is another trait universally preferred by females (Gerhardt & Huber, 2002). Finally, in grey treefrogs note efficiency shows positive temperature dependence, that is, much more of the metabolic energy consumed by the male calling muscles is being trans-

formed into acoustic energy at high temperatures than at low temperatures (McLister, 2001). All this suggests that the ability to place oneself in warmer environments for calling may be adaptive, and that temperature-based plasticity in calling site choice allows males to increase their metabolic efficiency and mate attraction effectiveness.

Data from our calling site choice experiments further suggests that grey treefrog males attend to the presence of predators, and that they adjust calling behaviour adaptively to reduce the chances of being detected. During the trials in which a predator was present, male treefrogs continued to preferentially settle in the warmer environment even if that meant being closer to a predator, but they largely refrained from calling. A range of predator taxa including bloodsucking insects, frogs, birds and mammals are reported to eavesdrop on frog calls in a predatory context (Jaeger, 1976; Tuttle & Ryan, 1981; Tuttle et al., 1981; Bernal et al., 2006; Iguane et al., 2008) suggesting that calling is a behaviour that makes males vulnerable to predators. Indeed, at our pond we have observed a bullfrog stalking and preying on a calling male grey treefrog. How grey treefrogs males perceived the proximity of the green frog in our trials is thus far unclear. Given our experimental setup, they may have used visual, olfactory, or water-wave cues. Because none of the green frogs called during the trials, acoustic cues did not seem to play a role here. Interestingly, during a study testing the effects of broadcasting bullfrog calls on the behaviour of grey treefrogs from another population, Schwartz et al. (2000) found that broadcast of bullfrog calls did not affect calling behaviour in males, or phonotaxis behaviour of female grey treefrogs towards a speaker broadcasting a conspecific call.

The frequency of spring peeper calls (3 kHz, Doherty & Gerhardt, 1984) falls within the auditory range of grey treefrogs (Diekamp & Gerhardt, 1995), and may thus interfere with effective communication. Nevertheless, the presence of acoustic competitors was not a major factor in determining calling site choice at our study. This is surprising, because most studies documenting calling sites choice do so in the context of spatial segregation between calling conspecifics. Maybe spatial segregation is more pronounced in the multi-species assemblages common in tropical location where many of those studies were conducted (i.e., Hödl, 1977; Luther, 2009; Schmidt et al., 2013), and the species diversity at our site was too low to result in sufficient competition for acoustic space. Then again, our examination of the

effect of acoustic competitors employed a rather coarse measure of competition in nature (i.e., nightly presence/absence of spring peepers), and we did not conduct behavioural trials similar to those conducted to assess the influence of predators on calling site choice. An investigation on a more local scale, say, involving measurements of nearest-neighbour distances between spring peepers and focal grey treefrogs, may have yielded different results. Alternatively, relatively low night-time air temperatures early in the Wisconsin breeding season may force a trade-off between avoiding acoustic competition and seeking preferred higher temperatures, with temperature preferences generally winning out. Later in the breeding season, or in southern areas of the species' distribution range where temperatures are generally higher, heterospecific competition may play a larger role in calling site selection. Indeed, a study conducted in Missouri found that grey treefrogs (*Hyla versicolor*) used ground calling sites (which were 1–2°C warmer than elevated sites) in allopatry, but in areas where they co-occurred with their sister species, the Cope's grey treefrog (*Hyla chrysocelis*) they used more elevated sites and thus achieved spatial separation from their competitor (Ptacek, 1992).

Calling in some species of anurans is one of the most energetically expensive behaviours known for any ectothermic animal (Wells, 2001), and any means of maximizing the efficiency and efficacy of this behaviour should be beneficial. In chorusing anurans this can be achieved in several ways. Because of the link between temperature and physiology in ectotherms, calling efficiency may be maximized by behavioural preferences for temperatures that increase the metabolic efficiency. Calling efficacy may be maximized by adaptive risk assessment, to decide when the proximity of a predator makes calling too dangerous to perform or when the din created by acoustic competitors decreases the benefit of calling for mate attraction. Here we have shown that grey treefrogs are capable of at least two of these options: they show temperature-based behavioural plasticity in calling site selection, choosing warmer calling sites, and they are capable of adaptive risk assessment, and often refrain from calling in close proximity to a predator.

Acknowledgements

This work was supported by funds from the University of Wisconsin–Milwaukee to G.H. Experimental procedures were approved by UWM's

IACUC protocol number 09-10#25. We thank the staff at UWM Field Station for logistic support and Rafael L. Rodríguez for helpful comments on the manuscript.

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