Effects of Increasing Temperature on Acoustic Advertisement in the Tettigoniidae

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Abstract

Acoustic communication in insects is vital for reproduction. In the family Tettigoniidae, certain features of acoustic signals are impacted by ambient temperature. The current study investigates the correlation between increased ambient temperature and signaling behavior in four species of katydids in two subfamilies under conditions that may be encountered as environmental temperatures continue to rise due to climate change. This is the first systematic investigation into the potential effects of temperature on song parameters in these four species. Individuals were tested at five different temperatures, ranging from 20°C to 40°C at 5°C intervals, and measurements were taken on six acoustic parameters: buzz duration, interbuzz interval (IBI) duration, number of ticks in the IBI, tick rate in the IBI, pulse rate within a buzz, and percent time spent calling. Results indicated a statistically significant effect of temperature on pulse rate, buzz duration, and interbuzz interval duration for all species tested. The percent time calling and buzz duration increased at higher temperatures in the single species in the subfamily Tettigoniinae, in contrast with the three species in the subfamily Conocephalinae which showed decreased percent time calling and reduced buzz duration in increased temperature. These results highlight the potential differences in the behavioral responses among different species to increasing global temperatures. Further research is necessary to assess the potential impact of variable calling parameters on female choice in these and other katydid species.

Key words

acoustic communication, katydid, female choice, climate change, *Metrioptera roeselii*, Conocephalinae, Tettigoniinae

Introduction

Acoustic signals are important for animal communication in many species, ranging from agonistic interactions to reproductive advertisements. In insects, the primary function of acoustic signals is to attract mates, often over long distances (Ragge & Reynolds 1998, Gerhardt & Huber 2002). These signals provide the receiver with information on caller attributes, such as species identification and quality, and aid in intraspecific interactions including male-male competition and female choice (Stiedl *et al.* 1991, Capinera *et al.* 2004). Insect sound production varies greatly between species and includes sounds produced via crepitation during flight, tremulation, and most commonly in the order Orthoptera, stridulation (Ragge & Reynolds 1998, Morris 1999, Capinera *et al.* 2004).

Members of the family Tettigoniidae (katydids) use stridulation as the predominant sound production mechanism by rubbing a scraper on the right forewing across a file on the left forewing (Dumortier 1963, Ragge & Reynolds 1998, Gwynne 2001). A pulse is the unit of sound produced during one muscle movement, or one opening or closing of the forewings (Gerhardt & Huber 2002). A single wing stroke usually produces one pulse of sound (Josephson & Halverson 1971), with one wing cycle producing a pulse on both the opening and closing of the forewings (Morris & Walker 1976). However, the correlation between wing cycles and sound production can be highly complex (Capinera *et al.* 2004) and some species produce only one pulse for every wing cycle (Dumortier 1963, Ragge & Reynolds 1998). Pulses of sound are grouped together in species-specific calling songs (Capinera *et al.* 2004). While the production mechanisms of orthopterans are fixed, and songs are highly stereotyped, there are aspects of male acoustic signals that are subject to individual variation (Ragge & Reynolds 1998). These characteristics include temporal properties, such as call duration and rate (Gerhardt & Huber 2002), and features that relate to body size, such as signal intensity (Bennet-Clark 1998).

Several studies have investigated species-specific female preference for those male-signaling behaviors that exhibit individual variation in katydids. Female preference for variable temporal properties has been well studied and both female *Amblycorypha parvipennis* and *Scudderia curvicauda* prefer longer phrases/buzzes (Galliart & Shaw 1992, Tuckerman *et al.* 1993, Galliart & Shaw 1996). Sound intensity is an honest indicator of body size in the Tettigoniidae (Bailey & Thiele 1983, Galliart & Shaw 1991), and females of several genera showed preferences for males that produced louder songs (Bailey 1985, Latimer & Sippel 1987, Galliart & Shaw 1991, Galliart & Shaw 1992). In contrast, females in the subfamily Zaprochilinae exhibited preferential phonotaxis towards males with higher carrier frequencies, an acoustic feature that corresponded to smaller male body size (pronotum length) (Gwynne & Bailey 1988). Age also seems to be an important predictor for female choice in some species. Female *Ephippiger ephippiger* (Stiedl *et al.* 1991, Ritchie *et al.* 1995) and *Mecopoda elongata* (Hartbauer *et al.* 2015) showed preference for acoustic signals associated with younger males. In general, female katydids seem to exhibit a preference towards longer buzzes, louder songs, and acoustic signal properties indicative of younger males.

Most insects are ectothermic, depending on external heat sources to regulate internal body temperature (May 1979, Gerhardt & Huber 2002). As a result, ambient temperature directly affects the physiology of ectothermic insects, including the neuromuscular system, and therefore acoustic signals (Gerhardt & Huber 2002). Cicadas and certain katydid species have the ability to generate body heat internally (May 1979, Gerhardt & Huber 2002). In these species, heat is generated by the active flight muscles (Heinrich 1974, May 1979). These same active flight muscles are used for sound production in species that stridulate to generate acoustic signals (Heinrich 1974, Elsner & Popov 1978, Josephson 1984). External temperature

will therefore have an impact not only on the initiation of calling song but also on aspects of acoustic signals that are controlled by temperature-dependent physiological mechanisms.

The effects of ambient temperature on the acoustic parameters of insect signals are well established for several orthopteran families and have extremely consistent results. In the late 1800's, research provided evidence that chirp rate increased with temperature in *Oecanthus* species (Dolbear 1897, Bessey & Bessey 1898) and continued work with this and other genera has complimented these early findings (Pires & Hoy 1992, Jang & Gerhardt 2007, Walker & Collins 2010). The impact of temperature on pulse rate has been extensively studied in many orthopterans with the majority of research demonstrating a linear or exponential relationship in both the Tettigoniidae (Frings & Frings 1957, Dumortier 1963, Spooner 1964, Walker 1975a) and Gryllidae (Walker 1962, Souroukis *et al.* 1992, Martin *et al.* 2000, Walker & Cade 2003, Jang & Gerhardt 2007, Walker & Funk 2014). In katydids, duration of phrases/buzzes (Frings & Frings 1962) has been shown to increase directly with temperature. Further, previous research has established a negative relationship between the duration of the interbuzz interval (Frings & Frings 1962, Arias *et al.* 2012) and percent time spent calling (Frings & Frings 1962) with increasing temperatures.

The current study describes the calling behavior of four katydid species representing three different genera under a wide range of temperature conditions, to assess their potential sensitivity to temperature changes.

Methods

Species descriptions.—The species chosen for the current study represent the genera *Metrioptera* [*Metrioptera roeselii* (Hagenbach, 1822) = *Roeseliana roeselii*], *Orchelimum* (*Orchelimum gladiator* Bruner, 1891), and *Conocephalus* [*Conocephalus brevipennis* (Scudder, 1862) and *Conocephalus fasciatus* (De Geer, 1773)]. *O. gladiator*, *C. brevipennis*, and *C. fasciatus* all belong to the subfamily Conocephalinae and *M. roeselii* belongs to the subfamily Tettigoniinae. A systematic investigation into the potential effects of temperature on acoustic parameters has not yet been carried out for any of the four species in the present study.

Species collection and husbandry.—Individuals were captured as either nymphs or adults in areas located around Syracuse, New York. Nymphs were housed together in Bug Dorms (BioQuip Products) and were moved to individual containers after their final molt. Age was recorded as the date of final molt for all individuals collected as nymphs. For individuals collected as adults, age was marked as unknown. Information on pronotum length, body length, and weight were collected after the completion of all tests and prior to death if possible. Insects were provided grass seed obtained from collection sites and were supplemented with Fluker's high calcium cricket feed as nymphs (Fluker Farm). All containers were misted at least once daily as a fresh water source. Individual and group houses were kept in a laboratory with a natural light/dark cycle, ambient temperature ~23°C.

Temperature tests.—Experimental trials were conducted using Exo Terra reptile egg incubators (Model PT2445, Rolf C. Hagen Corp.) with heating and cooling capability. Incubators were lined with 2" soundproofing acoustic foam (Part AP2-QTR, The Foam Factory) to dampen external noise and minimize reflections within the chamber. Recordings were made using Zoom H1 handy recorders (Zoom North America), sampled in stereo at 96kHz and 24-bit for all species. A built-in low cut (high pass) filter in the recorders was used to reduce the amount of low-frequency (<200Hz) fan noise that was produced by the incubators. Recorders were ~12cm away from the calling insect. Incubators were set to one of five temperatures: 20°C, 25°C, 30°C, 35°C, and 40°C (±1°C) and the temperature was monitored using calibrated thermometers (Model 14-648-46, Fisher Scientific). Temperatures were chosen to reflect the summer temperature range of the area and the published upper and lower tolerance limits of a closely related species (Heath & Josephson 1970). Humidity was not controlled for, however previous research has shown no correlation between humidity and wing-stroke rate (Walker 1975b). Individuals were placed in the incubator in their original housing to minimize disturbance. Trials were run for 1.5 hours with the initial 30 minutes used to acclimate the individual to the ambient temperature in the chamber. This 30-minute acclimation period was not used in the analysis and all measurements were made from the last hour of data collection. Each individual was tested at each temperature until it successfully called, with a maximum of three trials. If no calls were produced after three attempts, no further trials were conducted for that individual at that temperature.

Terminology.—In the current study, a *pulse* was defined as the sound produced by a single passing of the wings across one another (Dumortier 1963, Josephson & Halverson 1971), produced at regular intervals to make up a *buzz* (Morris & Fullard 1983, Walker 1975a, b). One wing cycle consists of two pulses (Morris & Walker 1976), therefore a *buzz* was considered to be a continuous series of two or more wing cycles not separated by more than the duration of two wing cycles. A *tick* was defined as the isolated unit of sound produced between buzzes (Morris & Fullard 1983). A *calling bout* was classified as a sequence of buzzes and/or ticks separated from another buzz or tick by more than 5 seconds. For those species that typically produced ticks between buzzes, calling bouts often consisted of multiple series of these buzz/tick sequences. Lastly, *calling song*, or simply song, was considered a complete sequence of sound, including both buzzes and ticks if applicable, that may consist of multiple bouts.

Acoustic analysis.—Recordings were analyzed using Raven Pro 1.5 (Cornell Laboratory of Ornithology) (2048 Hann window, 50% overlap, 1024 Hop size). All buzzes and, if applicable, individual ticks, were boxed according to bouts. The total duration of all bouts was summed and divided by the overall time of the trial to obtain a measurement of percent time calling. Within a bout, four acoustic parameters were measured, including buzz duration, interbuzz interval (IBI) duration, number of ticks in the IBI, and tick rate in the IBI. Within a buzz, pulse rate is consistent (Walker 1975a, b), and therefore we calculated this metric using a series of 10 pulses within a single buzz.

Statistical analysis.—Linear mixed-effects models (LMMs) were run in R (R Core Team 2015) to investigate the relationship between acoustic parameters and ambient temperature. This model accounts for pseudoreplication (repeated measurements on one individual) and non-normality. Random effects were considered to be ID of the individual, date, time of day, age, size, and weight, and the fixed effect was temperature. Using restricted maximum likelihood estimates (REML) to provide unbiased estimates of variance components, LMMs were run using the package lme4 (Bates *et al.* 2015).

Results

A total of 20 individuals were tested for each species. The number of individuals that had successful trials at each temperature can be found in Table 1. For *M. roeselii* mean (±SD) overall body length was 1.71±0.53cm, mean pronotum length was 0.43±0.13cm, and mean weight was 0.26±0.09g. For *O. gladiator* mean overall body length was 1.93±0.81cm, mean pronotum length was 0.46±0.19cm, and mean weight was 0.28±0.12g. For *C. brevipennis* mean overall body length was 1.30±0.41cm, mean pronotum length was 0.29±0.09cm, and mean weight was 0.10±0.03g. For *C. fasciatus* mean overall body length was 1.32±0.08cm, mean pronotum length was 0.27±0.03cm, and mean weight was 0.09±0.01g.

Description of acoustic signals.—The calling song of all four species consists of a series of buzzes composed of regularly spaced pulses (Fig. 1). The songs of *O. gladiator*, *C. brevipennis*, and *C. fasciatus* are further characterized by individual ticks during the inter-buzz interval, however these are absent in *M. roeselii*. Table 2 contains average values of each acoustic parameter and were based on songs produced at 25°C. The six acoustic parameters under investigation vary widely among the four species. Sound recordings are available on Orthoptera Species File Online (Eades *et al.* 2016).

Temperature effects on M. roeselii.—There was a significant effect of temperature on all four acoustic parameters (Table 3). Percent time calling and buzz duration increased as temperature increased, while interbuzz interval decreased as temperature increased (Fig. 2A,B,D). Buzz pulse rate increased linearly as temperature increased (Fig. 2C).

Temperature effects on O. gladiator.—There was a significant effect of temperature on four of the six measured parameters (Table 3). Both buzz duration and interbuzz interval decreased as temperature increased (Fig. 3B,D). The buzz pulse rate and the IBI tick rate increased as a function of temperature (Fig. 3C,F). There was no effect of temperature on the percent time spent calling or on the number of ticks between buzzes (Fig. 3A,E).

Temperature effects on C. brevipennis.—There was a significant effect of temperature on three of the six measured parameters (Table 3). Buzz duration and interbuzz interval decreased with increasing temperature (Fig. 4B,D) and buzz pulse rate increased with increased temperature (Fig. 4C). There was no effect of temperature on the percent time calling, the number of ticks between buzzes, or the IBI tick rate (Fig. 4A,E,F),

Temperature effects on C. fasciatus.—Temperature had an effect on all six of the acoustic parameters for *C. fasciatus* (Table 3). As temperature increased, percent time spent calling, buzz duration, interbuzz interval, and the number of ticks between buzzes all decreased (Fig. 5A,B,D,E). The buzz pulse rate and the IBI tick rate both increased with increased temperature (Fig. 5C,F).

Discussion

The effects of increasing environmental temperatures on four species in the family Tettigoniidae were investigated. All species tested demonstrated marked changes in acoustic signal parameters with temperature. There were statistically significant changes evident in pulse rate within a buzz, buzz duration, and interbuzz interval duration for all species. These results are consistent with previous findings of a relationship between these acoustic parameters and variation in temperature in katydids (Frings & Frings 1957, Frings & Frings 1962, Dumortier 1963, Spooner 1964, Walker 1975a, Arias *et al.* 2012).

All species in the current study showed an increase in pulse rate with increasing temperature. As pulse rate is dependent on wing-stroke rate, a physiological process that changes with temperature, these results are expected (Walker 1975a). Buzz duration was also affected by temperature in all four species, although different responses were observed in the Conocephalinae species compared to the one Tettigoniinae species. Specifically, a decrease in buzz duration was evident in the three Conocephalinae species. Since the thoracic temperature of singing katydids increases with ambient temperature (Heath & Josephson 1970), reduced calling time may be necessary at very high temperatures in order to maintain a thoracic temperature that does not result in overheating the body. Decreased buzz duration is also likely a compensation for the increased energy expenditure that occurs with increased temperature during calling song in insects (Prestwich & Walker 1981, Prestwich 1994). Interbuzz interval duration decreased with temperature in all four species tested. If an increase in temperature results in decreased buzz durations, decreasing the amount of time between buzzes might be a way to compensate and maintain a consistent percent time calling. A reduced interbuzz interval duration could therefore explain why male *O. gladiator* and *C. brevipennis* in the current study had no statistically significant changes in percent time spent calling despite the reduction in buzz duration. A decrease in buzz duration and interbuzz interval combined with an increase in pulse rate may also indicate that the calling song of katydids is both faster and compressed at higher temperatures.

Perhaps the most notable variation in response to increasing temperature was found in the response of *M. roeselii*; the three species in the subfamily Conocephalinae demonstrated a decrease in buzz duration while *M. roeselii* increased the duration of buzzes. *M. roeselii* also showed a significant increase in percent time calling at higher temperatures, even compared to *C. fasciatus*, the only other species with a statistically significant difference. *M. roeselii*, native to many parts of Europe, was introduced to North America prior to 1952 (Urquhart & Beaudry 1953). It is possible that it evolved under significantly different environmental conditions, contributing to the observed differential response to high temperatures compared to the three native North American species. Even species of katydids native to the same area exhibit different communication strategies and temperature responses however (Walker 1975a, b), so the observed responses may be more tied to the evolutionary relationship between these katydid subfamilies. These results em-

Table 1. The number of individuals that called successfully at each temperature.

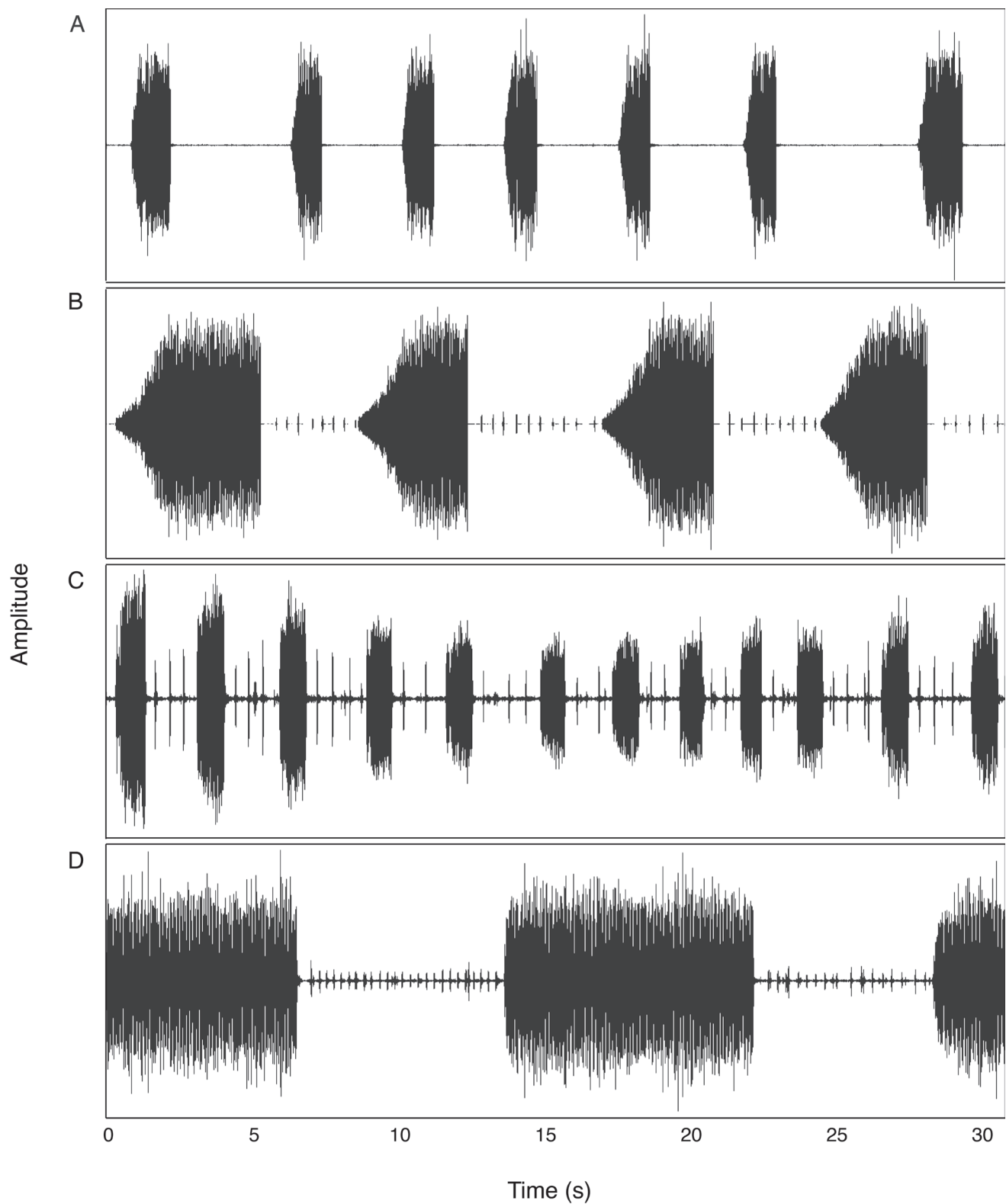| Species	20°C	25°C	30°C	35°C	40°C
M. roeselii	18	20	20	20	18
O. gladiator	17	19	18	19	17
C. brevipennis	5	20	19	20	12
C. fasciatus	20	20	20	20	20

Fig. 1. Visual representations (oscillograms) of the calling songs of the four species, A) *M. roeselii* B) *O. gladiator* C) *C. brevipennis* and D) *C. fasciatus*.

Table 2. Average values for the acoustic parameters investigated in all four species during the current study (mean±SD). All measurements were obtained from songs produced at 25°C.

Species	Percent Time Calling	Buzz Duration (s)	Interbuzz Interval (IBI) Duration (s)	Number of Ticks in IBI	IBI Tick Rate (ticks/s)	Buzz Pulse Rate (pulses/s)
M. roeselii	3.3±4.7	4.9±2.0	2.6±0.8	--	--	58.0±3.8
O. gladiator	36.3±34.2	3.9±1.5	4.0±1.5	5.5±3.4	1.4±0.7	27.1±1.1
C. brevipennis	35.6±35.0	1.2±0.5	1.8±0.5	2.4±1.0	1.4±0.4	40.9±2.9
C. fasciatus	83.5±25.0	14.0±15.8	6.0±1.5	19.6±7.6	3.3±0.9	28.3±1.7

phasize the difficulty in generalizing temperature responses across all Tettigoniidae.

Many male insects produce long-range signals that are subject to female choice, and males with the most attractive signals will be preferred (Gerhardt & Huber 2002). Changes in the acoustic signal parameters of calling song in the Tettigoniidae may therefore have important consequences for mate attraction and selection. Of the parameters investigated in the current study, female katydids have been shown to prefer males that produce longer buzzes. Buzz length may be indicative of important factors that constitute a good mate due to the increased energy expenditure required for longer buzzes (Greenfield & Shaw 1983). The buzz portion of katydid calling song is potentially the most localizable element (Guerra & Morris 2002), therefore longer buzz duration may also provide females with a better opportunity to locate a calling male. Males in the subfamily Conocephalinae significantly decrease the duration of the buzz components of their song, with *C. fasciatus* decreasing buzz duration by more than 92% from 20°C to 40°C. Decreased buzz duration could therefore have a negative impact on pairing in this subfamily due to a hindrance on localization. In contrast, *M. roeselii* increased not only the duration of the buzz but the percent time spent calling with increasing temperature, highlighting a potential benefit of rising environmental temperatures to this species.

Changes in acoustic parameters may also alter how the signal is perceived by females of related species. In sympatric species, distinctive song patterns are essential mechanisms of reproductive isolation (Alexander 1960). Almost all *Conocephalus* species share a carrier frequency which is the only portion of a signal that can be perceived from distant singing aggregations (Morris & Fullard 1983, Guerra & Morris 2002). Females must therefore rely on close range signals for species determination. In *C. brevipennis*, buzz discontinuity is required for correct discrimination between heterospecifics and conspecifics (Morris & Fullard 1983). If buzz duration was reduced at high temperatures in sympatric congeneric species, the altered signal might now elicit a phonotactic response from a *C. brevipennis* female and could potentially lead to interspecific breeding.

Despite published information on female choice in orthopterans, and in the Tettigoniidae in particular, the impact of changes in male acoustic parameters with temperature are poorly understood. Temperature coupling in many species ensures that an acoustic signal will be matched between the sender and receiver despite changes in temperature (Gerhardt 1978). This phenomenon has been observed in both crickets (Doherty 1985, Pires & Hoy 1992) and grasshoppers (Helversen & Helversen 1981). In the katydid *Neoconocephalus triops*, males demonstrated developmental plasticity in their calls which allowed for a match between female preference and the calling songs of males (Beckers & Schul 2008).

Female preference in katydids is both highly variable and difficult to generalize across taxonomic groups. More research is necessary to further examine the relationship between the acoustic features tested here and female choice. Rising global temperatures, as well as increased stochasticity, are likely to have profound effects on ectothermic organisms (Porter *et al.* 1991, Harrington *et al.* 2001). Impacts on acoustic signaling behavior may include the onset and

Table 3. Results of the LMMs. Statistical significance (p<0.05) is denoted with an asterisk.

| Species	Metric	Estimate	Std. Error	df	t-value	Pr (>|t|)	
M. roeselii	Percent Time Calling	1.893	0.349	75.10	5.430	6.67E-07	*
	Buzz Duration	1.193	0.450	73.41	2.649	0.010	*
	IBI Duration	-0.082	0.020	40.35	-4.076	2.09E-04	*
	Buzz Pulse Rate	3.206	0.063	65.37	50.520	<2.00E-16	*
O. gladiator	Percent Time Calling	0.181	0.429	58.54	0.421	0.675	
	Buzz Duration	-0.208	0.020	58.84	-10.180	1.35E-14	*
	IBI Duration	-0.120	0.026	54.62	-4.579	2.74E-05	*
	Number of Ticks in IBI	-0.085	0.057	57.29	-1.483	0.144	
	IBI Tick Rate	0.039	0.013	58.05	2.913	0.005	*
	Buzz Pulse Rate	1.521	0.031	67.62	49.660	<2.00E-16	*
C. brevipennis	Percent Time Calling	-0.685	0.683	64.20	-1.003	0.320	
	Buzz Duration	-0.054	0.007	60.42	-7.604	2.23E-10	*
	IBI Duration	-0.048	0.016	51.33	-3.044	0.004	*
	Number of Ticks in IBI	-0.026	0.029	49.93	-0.880	0.383	
	IBI Tick Rate	0.013	0.014	50.15	0.886	0.380	
	Buzz Pulse Rate	2.357	0.082	52.66	28.730	<2.00E-16	*
C. fasciatus	Percent Time Calling	-0.721	0.326	81.01	-2.213	0.0297	*
	Buzz Duration	-1.684	0.336	65.89	-5.007	4.38E-06	*
	IBI Duration	-0.404	0.034	63.54	-11.890	<2.00E-16	*
	Number of Ticks in IBI	-0.545	0.095	67.70	-5.737	2.46E-07	*
	IBI Tick Rate	0.152	0.012	65.83	12.369	<2.00E-16	*
	Buzz Pulse Rate	1.734	0.036	88.85	48.441	<2.00E-16	*
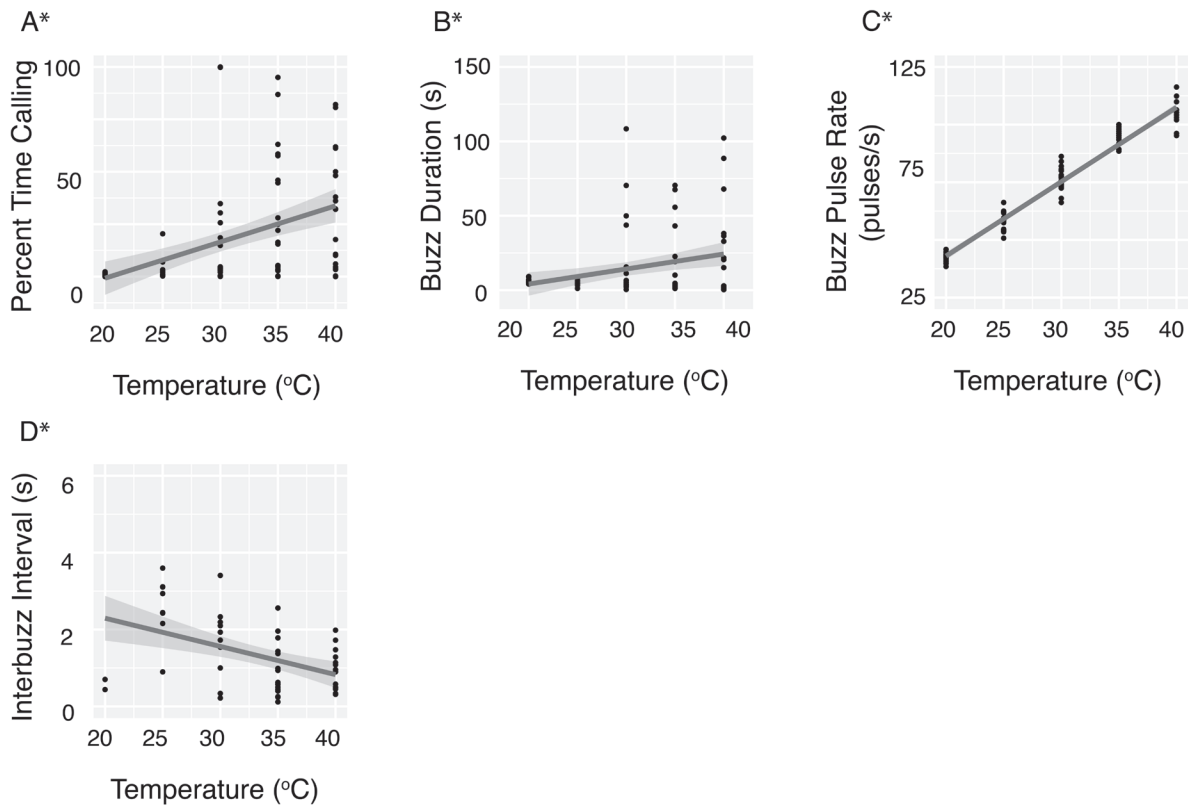
Fig. 2. The effects of increasing temperature on four acoustic parameters in *M. roeselii.* Statistical significance (p<0.05) is denoted with an asterisk.

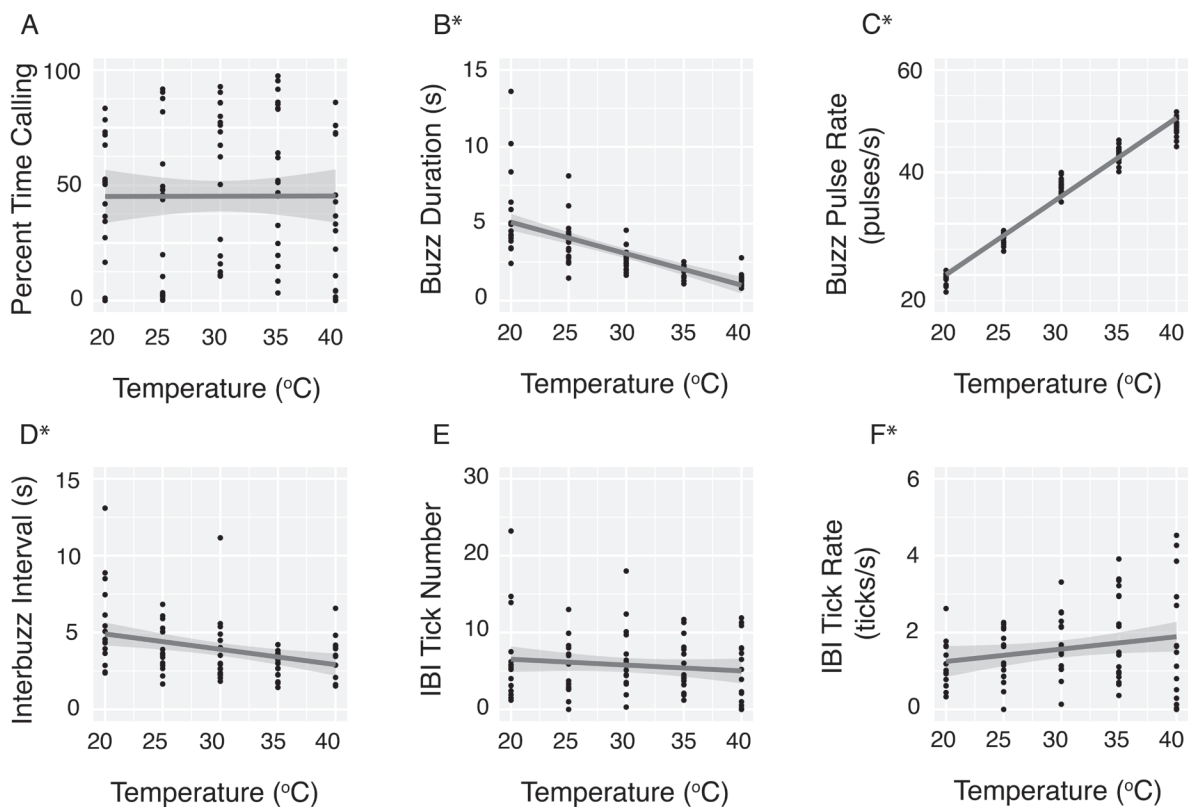**Fig. 3.** The effects of increasing temperature on six acoustic parameters in *O. gladiator.* Statistical significance (p<0.05) is denoted with an asterisk.
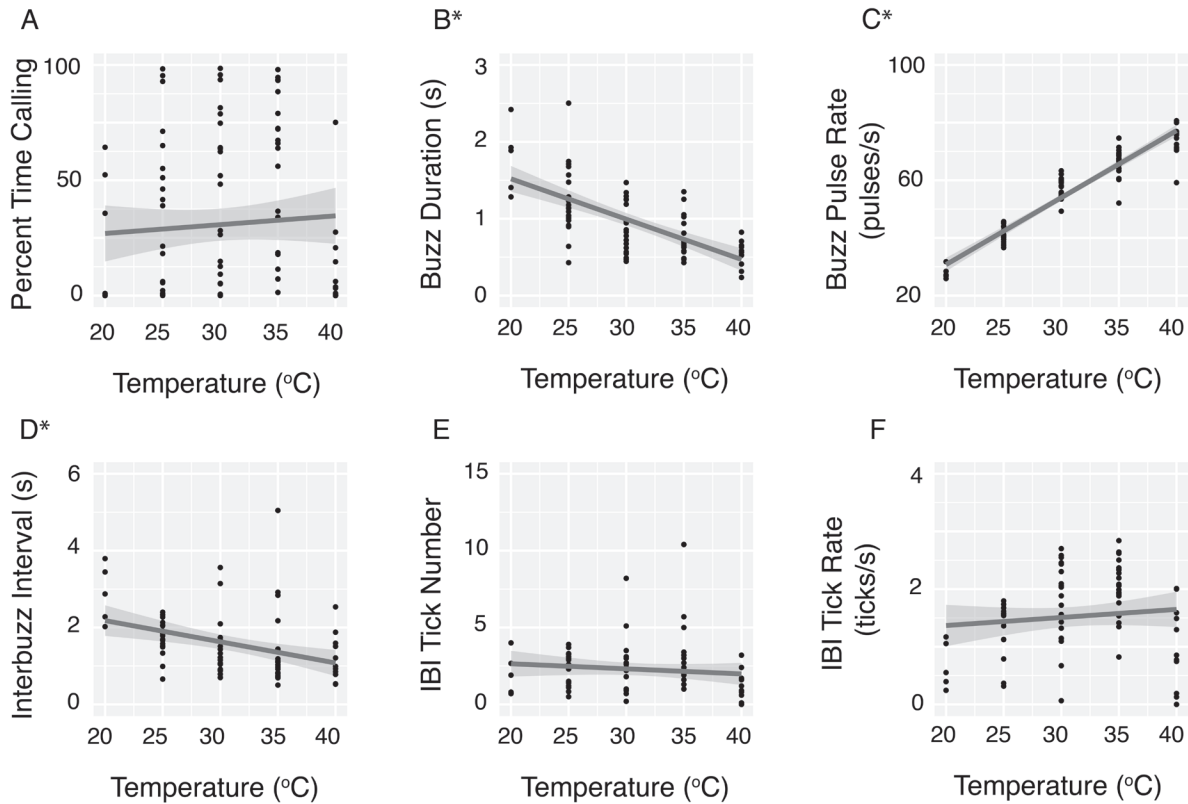
Fig. 4. The effects of increasing temperature on six acoustic parameters in *C. brevipennis.* Statistical significance (p<0.05) is denoted with an asterisk.

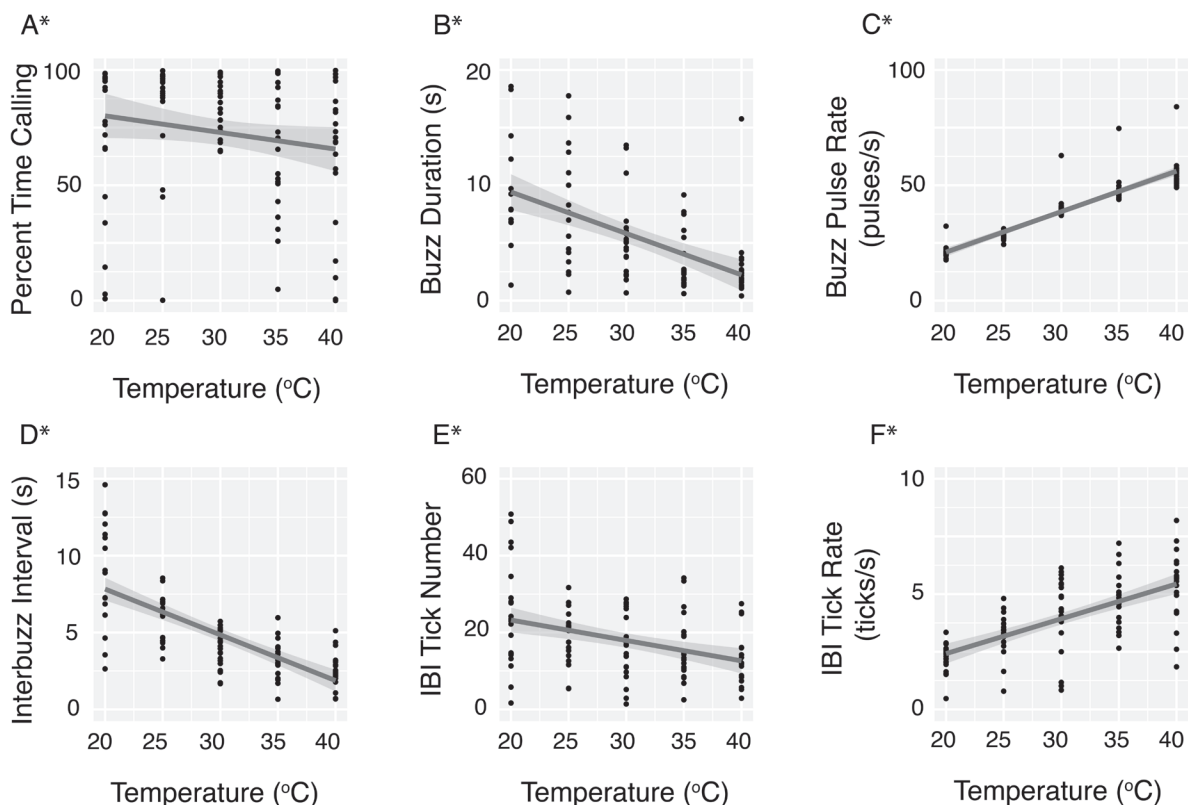**Fig. 5.** The effects of increasing temperature on six acoustic parameters in *C. fasciatus.* Statistical significance (p<0.05) is denoted with an asterisk.

timing of seasonal calling activity and an increase in the percent time spent calling throughout a season. Future studies will be focused on the responses of female katydids to changes in acoustic parameters over variable temperature ranges. The results of these experiments will help to shed light on how rising temperatures may ultimately impact mating behavior in these species.

Acknowledgments

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