*Spring Field Crickets (*Gryllus veletis*) Use Two Different Pulse Types When Signaling to Attract Mates*

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Spring Field Crickets (*Gryllus veletis*) Use Two Different Pulse Types When Signaling to Attract Mates

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Abstract Male field crickets acoustically signal to attract females by raising their forewings and rubbing them together to produce "regular" (lemon-shaped) pulse sound waveforms. In contrast, we have observed that spring field crickets, *Gryllus veletis*, often produce an irregularly shaped pulse that exhibits a complete drop in amplitude near the center of the pulse, termed "gap pulses." We tracked the occurrence of regular and gap pulses temporally. Males change how they signal through time, producing increasingly more gap pulses later in the night and in the morning than through the afternoon and evening. Wing wear did not explain variation in gap pulse production. However, variation in gap pulse production is attributable to variation in body size, with larger males that signal with longer chirps and at lower carrier frequencies producing relatively more gap pulses than smaller males. We hypothesize possible proximate and ultimate causes for the production of gap pulses.

Keywords Orthoptera · Gryllidae · Gryllinae · *Gryllus veletis* · gap pulses · split syllables · pulse · signal · wing wear · wing damage

Introduction

Male crickets produce acoustic signals to attract potential mates from a distance. Females typically display phonotaxis towards males that signal with the greatest effort (Cade 1979; Crnokrak and Roff 1995; Hunt et al. 2004) and mating success is partially dependent on their signals' acoustic properties. For example, females are attracted to males that signal most often in *Gryllus integer* (Cade and Cade 1992), *G. campestris* (Holzer et al. 2003), and *Teleogryllus commodus* (Brooks et al. 2005; Bentsen et al. 2006). Females are also attracted to males that signal with long bout durations (*G. integer*: Hedrick 1986; Leonard and Hedrick 2010), long pulse durations (*Laupala cerasina*: Shaw and Herlihy 2000), and high chirp rates and long chirp durations (*G. lineaticeps*: Wagner 1996). Sexual selection therefore has great

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potential to influence the type and attributes of male acoustic signals. Here we describe a novel pulse type that male spring field crickets, *Gryllus veletis*, often use when signaling to attract a mate.

Males produce acoustic long distance mate attraction signals by raising their forewings (tegmen) and rubbing them together (for descriptions of cricket stridulation see Walker 1962; Martin et al. 2000; Elliott et al. 1983; Koch et al. 1988; Prestwich and O'Sullivan 2005) typically resulting in "regular" (lemon-shaped) sound pulses (Fig. 1). *Gryllus veletis* field captured (L. Fitzsimmons pers. com.) and laboratory-reared males also frequently produce irregular pulse waveforms termed "gap pulses" (Fig. 1), sensu Schneider and Hennig (2012). Gap pulses exhibit a drastic drop in amplitude mid-way through the pulse. We argue that since gap pulses display drops in amplitude that have durations of around 5–10 ms, whereas the average interpulse durations that we observed were much larger (: x±SD=33.8±0.1 msec, min= 18.9 ms, max=49.2 ms), gap pulses represent a new type of pulse (Fig. 2). Here we provide a definition of, and method to identify, gap pulses for *G. veletis* and provide proximate and ultimate hypotheses for their production.

Proximately, gap pulses could result from random mechanical errors in stridulation. This "null" hypothesis predicts that the proportion of gap pulses should not be correlated with body size or signaling differences and should not change as individuals tire or age. Gap pulses have been occasionally observed in other cricket species (Hartley and Stephen 1989; Jang and Gerhardt 2006), and Hartley and Stephen (1989) hypothesized that gap pulses result from loss or degradation of teeth from the mid-section of the stridulatory file. This "stridulatory wear" proximate hypothesis predicts that 1) males should produce more gap pulses with increasing age resulting from increased wing wear, 2) males that produce gap pulses have stridulatory files

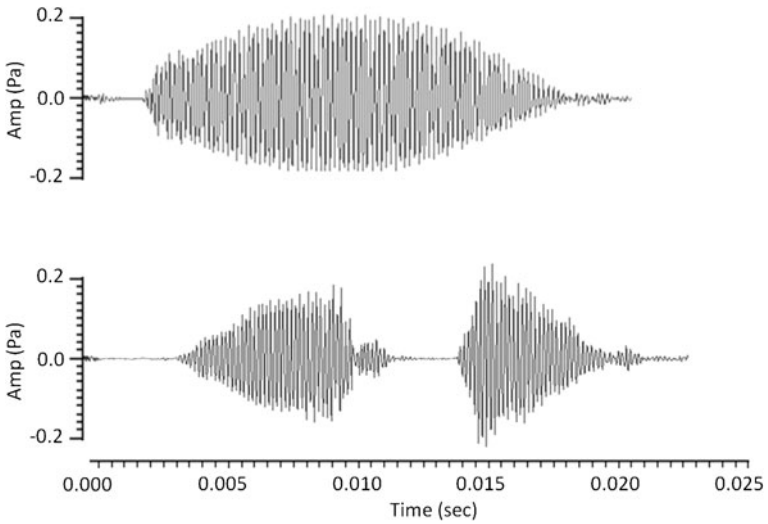

Fig. 1 *Top* regular pulse: common waveform of long distance mate attraction signaling. *Bottom* gap pulse: to be considered a gap pulse the amplitude in the gap must drop to 1/5 or less of the amplitude of the first pulse, the amplitude of the post-gap pulse must be at least 1/4 the amplitude of the pre-gap pulse, and the post-gap pulse must be at least 1/4 of the length of the pre-gap pulse. Both pulses are from the same individual during the same night and represent the middle pulse within a chirp

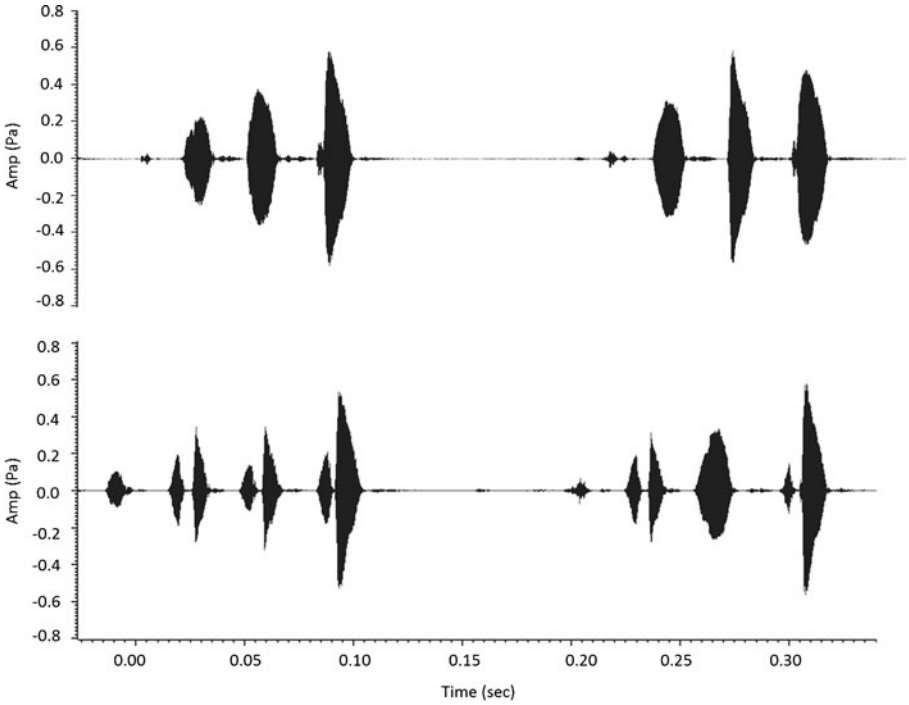

Fig. 2 *Top* Chirp containing only regular pulses. *Bottom* Chirp containing split pulses and a regular pulse. Both chirps were recorded from the same individual in the same night

with missing or degraded teeth, and 3) once males start producing gap pulses they should not switch back to producing regular pulses.

Beside the aforementioned proximate hypotheses (null and stridulatory wear), gap pulse might be somehow evolutionarily favored. Males that produce gap pulses may be changing their signaling in a way that is more attractive to females, such as increasing the length of their chirps (Wagner 1996; Shaw and Herlihy 2000). This "attractiveness" hypothesis predicts that females prefer chirps with gap pulses over chirps with regular pulses, gap pulses are longer than regular pulses, and chirps that contain one or more gap pulses are longer than chirps that contain only regular pulses. The "attractive" hypothesis may also predict that gap pulses are more energetically costly to produce than regular pulses, thereby acting as an honest display of male condition. Conversely, gap pulse production may be less energetically costly for males. This "energetic" hypothesis predicts that males will produce more gap pulses as they tire, and gap pulse production is less costly than regular pulse production. The energetic costs of acoustic signaling depend upon a number of factors, one of which is the number of teeth struck with every motion of the plectrum along the stridulatory file (Prestwich and Walker 1981). Tooth thickness may also influence the energetic costs of stridulation as it should be more energetically expensive to strum thicker teeth. If males can eliminate the most costly stroke-actions by not stroking the teeth at the center of the file, then they may decrease the energetic cost of each pulse.

By determining the acoustic signaling properties and temporal patterns of gap pulse production, we test a subset of the aforementioned predictions to gain insight

into potential proximate and ultimate explanations for why this unusual form of mate attraction signaling occurs. Here we (1) quantify variation among males in gap pulse production and determine if it occurs randomly or is correlated with differences in body size or acoustic signaling properties. (2) We quantify temporal variation within males in gap pulse production and determine if gap pulse production occurs randomly or if individuals change the proportion of gap pulses they produce throughout the course of the night or throughout the course of a week. If gap pulses result from fatigue, we predict there should be more gap pulses produced in the later part of the night. If gap pulses result from wear of signaling apparatuses, we predict crickets will produce increasingly more gap pulses with age. (3) We quantify the length of both regular and gap pulses to determine whether gap pulses are longer.

Methods

We conducted our study in accordance with the guidelines of the Canadian Council on Animal Care. Male *G. veletis* adults were collected in Mississippi Mills, Ontario, Canada in June, 2010 and housed at Carleton University, Ottawa, Ontario, Canada. No permits were required to collect *G. veletis*. Crickets were reared in species-specific communal 68 L (64 cm×40 cm×42 cm) plastic bins with a controlled temperature of 25±2 °C and a 14 h light:10 h dark cycle. Crickets were provided with ad libitum water and food (Harlan Teklad Rodent diet, 8604 M, Madison, WI, USA), stacked egg cartons for shelter, and moist sand for ovipositing. Juvenile crickets were held in separate communal bins from adults to reduce the chance of density induced cannibalism on the smaller individuals.

Fourth generation juvenile crickets were checked daily for individuals that had undergone imaginal moult (identified by the presence of fully formed wings). The day they reached adulthood, 22 males in total, newly moulted males were housed individually in 520 mL clear plastic containers (11 cm diameter×7 cm height) and under the same illumination and thermal environment that they experienced during rearing. They were each provided with a shelter (crumpled unbleached paper towel). Square holes (4 cm×4 cm) were cut out of the lids of the containers and wire mesh was put in place to allow air and sound to pass through.

Seven days post imaginal moult, males were transferred to a real time electronic acoustic recording system (EARS II: designed and built for our laboratory by Cambridge Electronic Design Ltd., Cambridge, UK). Each male was placed inside a Styrofoam cooler box with 2.5 cm thick walls lined with 2.5 cm thick acoustic foam to virtually eliminate sound contamination from neighbouring males. Each box was equipped with an LED light which provided the same 14 h light:10 h dark cycle experienced during rearing. Each box was also equipped with a microphone (electret condenser type KECG2742PBL-A; Kingstate Electronics, Tamshui, Taipei, Taiwan) that was positioned next to the LED light, 6.6 cm above the top of the male's housing container. Microphones recorded the acoustic signaling properties of each male in real time. The CricketSong software (Cambridge Electronic Design Ltd., Cambridge, UK) monitored the signaling parameters for each male cricket and provided an hourly summary of time spent signaling (min) and mean pulse duration (ms), interpulse duration (ms), number of pulses per chirp, chirp duration (ms), interchirp duration

(ms), carrier frequency (Hz), and amplitude (recorded in Pascals that were subsequently converted to decibels). Additionally, the CricketSong software scanned each hour that a cricket signalled and saved each cricket's 30 s interval with the highest calling effort as a WAV file. Cricket signaling was recorded for 7 days (7–14 days post imaginal moult).

We used Spike 2 software (Cambridge Electronic Design Ltd., Cambridge, UK) to view male WAV files. We inspected the first 100 pulses in each 30 s WAV file recording and quantified the proportion of regular shaped pulses and gap pulses. We used three specific criteria when determining if a pulse qualified as being a gap pulse (Fig. 1). First, the amplitude in the gap must drop to 1/5 or less of the amplitude of the pre-gap pulse, second, the amplitude of the post-gap pulse must be at least 1/4 the amplitude of the pre-gap pulse, and third, the post-gap pulse must be at least 1/4 of the length of the pre-gap pulse (Fig. 1).

We analyzed the number of gap pulses produced on two temporal scales: (1) every hour within one 24-h period (from noon on day 12 to noon on day 13) to test the prediction that males produce more gap pulses as they become fatigued, and (2) across days (during the hour from 02:00–03:00) to test the prediction that males produce more gap pulses with age and wing wear. We chose day 12 to day 13 for our hourly analysis and 02:00–03:00 for our daily analysis because the highest proportion of crickets signaled during these time periods. To identify differences in pulse durations we quantified the duration of 10 regular shaped and 10 gap pulses from 18 different individuals.

At 14 days post imaginal moult each cricket's dorsal side was photographed using a Zeiss Discovery V12 microscope and accompanying Axiovision software (version 4.8.2.0, Carl Zeiss MicroImaging, Jena, Germany). The dorsal photograph was used to quantify in μm each male's pronotum width, length, and area, along with head capsule distance (distance between the outer edges of each eye). We used a principal component analysis (PCA) to reduce all size measures into an orthogonal axis. The first principal component accounted for 90.3 % of the variation in body size measurements (Size PC1; Eigenvalue=3.613) and all morphological measures loaded heavily onto this first principal component. All other principal components had Eigenvalues <0.35.

We dissected all crickets at 14 days post imaginal moult and removed their forewings. We examined each cricket to determine which wing (left or right) was positioned on top to identify the file used for stridulation. All but one cricket positioned their right wing above their left. We then used scanning electron microscopy (SEM) to examine the detailed ultra-structure of the file on the underside of the top wing of each cricket to determine wear or damage to the teeth using a Tescan Vega-II XMU SEM (Tescan, Brno, Czech Republic). The files on each cricket's wings were first coated with an ultrathin electrically conducting gold/palladium (60 %/40 %) film deposited using plasma sputter using a Hummer VII sputter system (Anatech USA, Union City, CA, USA).

All statistical analyses were performed in SPSS v19.0.0 (SPSS Inc., IBM Company). To determine whether variation among males in gap pulse production was related to body size, signal quantity, or fine-scale signaling structure, we ran a generalized linear model with average number of gap pulses produced over the course of the week as the dependent variable and male size (PC1) and average time spent

signaling, chirp duration, interchirp duration, amplitude and carrier frequency as covariates. We did not include pulse duration, interpulse duration, or pulses per chirp in the generalized linear model since the EARS II system would sometimes record a gap pulse as two distinct pulses. Further it does not discern between a gap and an interpulse, under-representing the pulse duration and interpulse duration, and over-representing the number of pulses in the chirp. All signaling parameters were normally distributed (Shapiro-Wilks Goodness-of-Fit test).

To determine whether variation within males in gap pulse production was related to age or time of day we used general linear mixed models with repeated measures on the hourly or daily (age) number of gap pulses produced. The models included male identity as a random effect, male size (PC1) as a covariate, time (hour or day), and a time by size interaction as independent factors. The time by size interactions in both models were non-significant and were excluded from the analyses following Engqvist (2005). To ascertain whether gap pulses were longer than regular pulses we used a general linear mixed model with male identity as a random effect and pulse type (regular or gap) as the categorical dependent variable.

Results

Males exhibited considerable variation in how often they produced gap pulses, with the distribution being non-normal (Shapiro-Wilks, $W=0.878$, $p=0.011$) and positively skewed (Fig. 3). Males that produced the most gap pulses in their lifetime were larger, and produced signals with longer chirp durations and lower carrier frequencies (Table 1). Gap pulses were significantly longer than regular pulses (gap: $x\pm SD=23.5\pm0.4$ msec, regular: $x\pm SD=21.1\pm0.4$ msec; $p<0.0399$, $F=5.005$, $R^2_{adj}=0.368$, df=1.18). We found no discernible differences in wear or damage to the teeth of stridulatory files between any of the crickets using SEM (Figs. 4 and 5). The material between the teeth of crickets could be either smooth (Fig. 4) or irregular (Fig. 5), but these differences were not consistent across individuals that produced gap pulses and those that did not. *Gryllus veletis* males switched back and forth between producing gap and regular pulses, with individuals altering the proportion of gap pulses they produced through the course of the day (Table 2). Gap pulse production seemed to increase in the morning hours from lights on at 06:00 until midday (Fig. 6). Males did not, however, alter their gap pulse

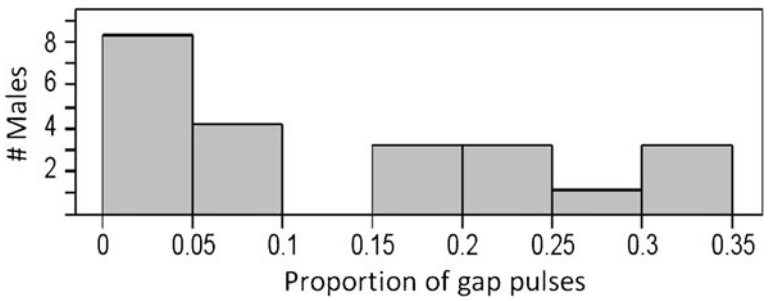

Fig. 3 Frequency distribution of average proportion of gap pulses produced per individual over the course of the 7-day monitoring period. Distribution is non-normal and skewed to the right

Table 1 Generalized linear model for the effect of average fine scale signaling parameters and size on the number of gap pulses produced

Model parameter	Slope	SE	X^2	DF	p
Whole model			22.215	6, 14	<0.0001
Time spent signaling	−0.019	0.018	1.096	1	0.2950
Chirp duration	0.338	0.098	11.967	1	0.0005
Interchirp duration	−0.020	0.014	2.051	1	0.1521
Carrier frequency	−0.012	0.006	4.197	1	0.0405
Amplitude	0.471	0.252	3.501	1	0.0613
Size	3.102	0.791	15.370	1	<0.0001

production as they aged throughout the course of the week that they were monitored (7–14 days post imaginal moult; Table 3).

Discussion

Male *G. veletis* often produce gap pulses when they signal to attract a mate. While substantial variation exists among males in their gap pulse production, gap pulses do not occur at random as predicted by our null hypothesis or later in life as predicted by our stridulatory wear hypothesis. Instead, variation in gap pulse production correlates with variation in body size and signaling properties (Table 1). Larger males that signaled with longer chirp durations and lower carrier frequencies produce more gap pulses in their lifetime (Table 1).

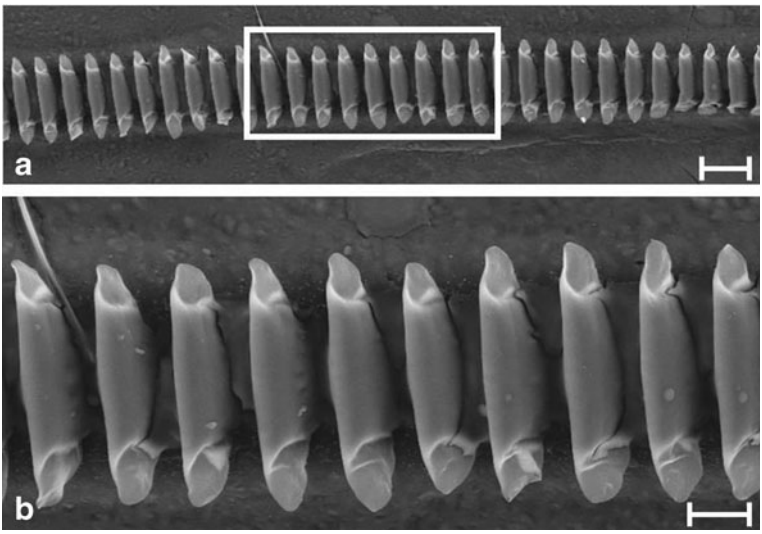

Fig. 4 SEM photographs of the file and teeth from the underside of the right wing of a male *G. veletis* that performed no gap pulses. **a** Center of the file at 200× magnification. *Scale bar* represents 50 μm. **b** Detailed view of the central teeth of the file at 600× magnification. *Scale bar* represents 20 μm

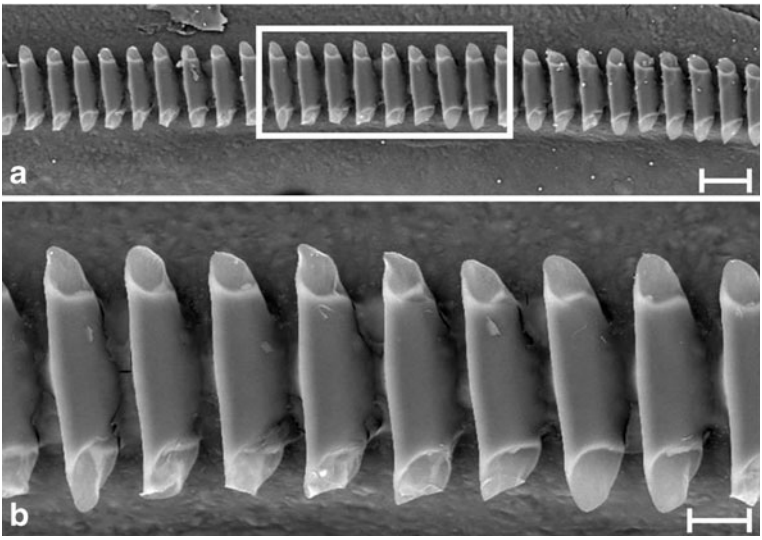

Fig. 5 SEM photographs of the file and teeth from the underside of the right wing of a male *G. veletis* that performed the most gap pulses observed (33 % of all pulses examined). **a** Center of the file at 200× magnification. *Scale bar* represents 50 μm. **b** Detailed view of the central teeth of the file at 600× magnification. *Scale bar* represents 20 μm

Why do males produce gap pulses? Hartley and Stephen (1989) found gap pulses in a bush cricket, *Poecilimon schmidti*, and attributed production to wear of the stridulatory file. We used SEM to examine the files and teeth of all of the crickets in our study, and found no discernible difference between crickets that produced and those that did not produce gap pulses (Figs. 4 and 5). Our males also regularly switched between gap and regular shaped pulses, further suggesting that the stridulatory wear hypothesis may not be the underlying proximate explanation for gap pulse production in *G. veletis*.

Gap pulse production could instead result from males pausing their wing movements mid-closure, changing the angle of their wings mid-closure, or reducing the force with which the plectrum strikes the file mid-closure. Since loss of wing contact can create gaps in sound production (Schneider and Hennig 2012), future research should investigate changes in wing angle or the pressure between file and scraper as proximate mechanisms to account for the drop in amplitude in the mid-section of the pulse.

The ultimate implications of gap pulses also require further exploration. Our findings revealed that males produced more gap pulses after midnight and throughout the morning, typically following a whole night of signaling (Fig. 6). This trend was

Table 2 Repeated measures model of the effects of size and time of day (time) on the number of gap pulses produced. Individual was included as a random effect and explained 3.9 % of the total variation

Source	F-ratio	DF	p	R^2_{adj}
Size	3.5501	1, 20	0.0742	0.110
Time	11.5931	1, 262	0.0008	

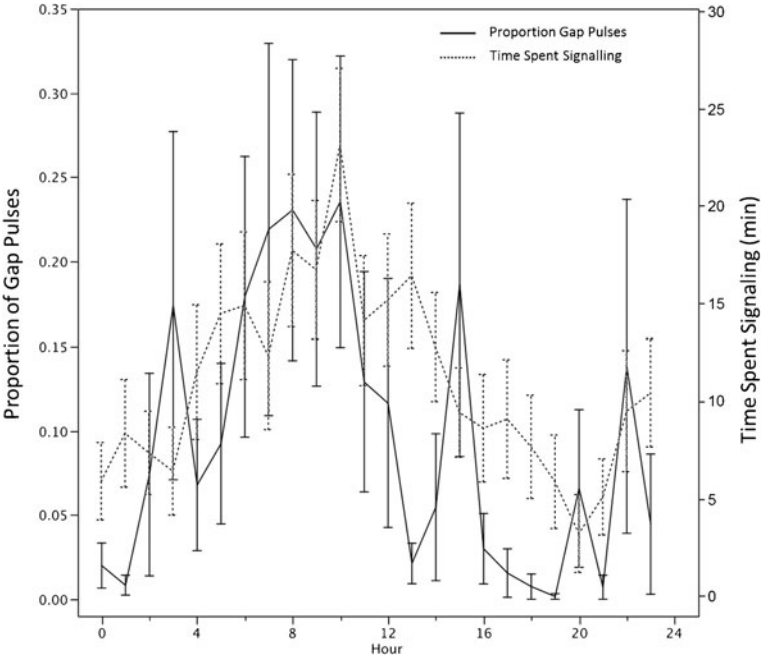

Fig. 6 Average hourly time spent signaling and percent gap pulses produced over one 24 h period. Males signaled more and produced more gap pulses later in the night and in the early morning. *Error bars* represent standard error

consistent over the course of the week, with there being no effect of day on gap pulse production (Table 3). Gap pulse production could, therefore, be an artifact of muscular fatigue, especially in larger males, providing some support for the "energetic" hypothesis. Gap pulses may be a subtle way for a male to save energy while signaling for a mate, especially if mid-closure changes of wing angle or force reduce the energetic demands on the signaling male. However, since we do not know how energetically demanding gap pulses are to produce, it is also possible that gap pulses could be more energetically demanding than regular pulses and could therefore act as an honest signal. Previous work on field captured *G. veletis* shows that males plastically adapt their signals to be most attractive when females are most active (Bertram et al. 2013). We found that female *G. veletis* mating activity in the wild (French and Cade 1987) aligns with gap pulse production in our study which could indicate that gap pulse production is one method for males to plastically adapt their behavior to their environment. The honest display hypothesis is further substantiated

Table 3 Repeated measures model of the effects of size and age on the number of gap pulses produced. Individual was included as a random effect and explained 2.4 % of the total variation

Source	F-ratio	DF	p	R^2_{adj}
Size	1.7389	1, 15	0.2074	0.091
Age	1.1734	1, 59	0.2831	

by the fact that the males that produce the most gap-pulses in their lifetime are larger and signal with greater effort and more attractive fine scale components (Table 1).

Preference tests to determine how females respond to males producing gap pulses compared to males producing regular pulses have yet to be conducted in *G. veletis*. If female *G. veletis* preferentially mate with males that produce longer pulses and/or longer chirps, then males that produce gap pulses might be more attractive, as gap pulses are longer than regular pulses and result in longer chirp durations (Figs. 1 and 2). Research on a different species found that *G. bimaculatus* also produce gap pulses (Schneider and Hennig 2012), although neither the drop in amplitude nor the duration of the second pulse appear as pronounced as they do in *G. veletis*. Female preference tests in *G. bimaculatus* reveal that while the gaps in the pulses are large enough to be detected by the females' auditory processing, gap pulses do not influence female preference (Schneider and Hennig 2012).

Overall our findings reveal that gap pulse production is non-random. Instead, gap pulse production is correlated with male size as well as fine scale properties of long distance mate attraction signals, although this may be an indirect consequence of certain acoustic parameters being themselves closely related to size. Our findings also reveal that gap pulse production increases throughout the night, possibly due to fatigue or to enhance mating success during times that most mating occurs in the wild. By quantifying the energetic demands of gap pulses compared to regular shaped pulses and the effect producing gap pulses has on a male's attractiveness, future research should determine if gap pulses are a novel signaling strategy with significant adaptive implications.

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