

# Signaling effort does not predict aggressiveness in male spring field crickets

Lauren P. Fitzsimmons · Susan M. Bertram

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**Abstract** The relationship between signaling and aggression is still unclear despite several decades of research. However, there is a growing interest in studying signals that predict aggressive behavior or fighting ability. The goals of our study were threefold: we investigated the relationship between signaling effort and aggression, the relationship between body condition and aggression, and the effect of fighting experience on subsequent signaling behavior in wild-caught and laboratory-reared male spring field crickets (*Gryllus veletis*). We found that aggressive behavior was not related to signaling effort, body size, or body condition. For contest winners, wild-captured males were more aggressive than laboratory-reared males. Signaling effort was highly repeatable within individuals, but aggressive behavior had low repeatability. We found no evidence for a winner or loser effect on signaling; there was no change in signaling effort when we compared contest winners and losers before and after they participated in aggressive contests. Long-distance acoustic signaling and aggressive behavior appear to be independent of one another in spring field crickets, perhaps serving different functions in female attraction and male–male competition, respectively.

**Keywords** Aggression · Acoustic signaling · Contests · Sexual selection

## Introduction

Nonlethal patterns of settling disputes, such as agonistic displays and ritualized fighting, have likely evolved because such behaviors benefit the individuals engaged in the

disputes (Maynard Smith and Harper 2003). Aggression is generally regarded as a behavioral strategy for asserting claim to a limited resource, such as a territory or a mate, to increase reproductive success (Cunningham and Birkhead 1998). For agonistic displays to be reliable, only those individuals who can back them up with physical displays should use them. Enquist (1985) suggested that honest signaling can occur in competitive situations due to the potential cost of fighting against a strong individual, contrary to earlier models that emphasized that such displays could not form evolutionary stable strategies due to the ease of bluffing (Maynard Smith 1974). While selection should favor reliable displays that signal information about the fighting ability or aggressive intent of competitors, low levels of deception are expected to occur (Számádó 2008).

Recently, Searcy and Beecher (2009) highlighted that, while there are many animal signals that are thought to function as agonistic displays, there is little empirical evidence that these signals provide information about the fighting ability or aggressive intent of individual signalers. For example, there is mixed, but predominately negative, evidence that song-type matching or song overlapping predicts aggression in songbirds (Searcy and Beecher 2009). Notable exceptions to this generalization include changes in call frequency as an honest indicator of fighting ability in frogs (Wagner 1992) and low-amplitude song as a threat signal predicting imminent attack in songbirds (Searcy et al. 2006; Ballentine et al. 2008; Hof and Hazlett 2010). Researchers have thus been prompted to provide evidence that behaviors we assume to serve as aggressive signals do indeed predict fighting ability or aggressive intent (van Staaden et al. 2011).

Most studies examine the mechanisms of sexual selection in isolation, but this approach can result in a misleading understanding of the total strength and form of sexual selection on male traits (Hunt et al. 2009). Our study focuses on whether acoustic signaling behavior is related to fighting ability in crickets. It is important to examine how signaling is related to male–male competition to more accurately

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L. P. Fitzsimmons (✉) · S. M. Bertram  
Department of Biology, Carleton University,  
1125 Colonel By Drive,  
Ottawa, ON K1S2Y4, Canada  
e-mail: lauren.p.fitzsimmons@gmail.com

assess some of the selective forces acting on male signaling. Research on the signaling behavior of crickets has been extensive, but studies of agonistic behavior are relatively less common. Further, the evidence for a relationship between long-distance mate attraction signaling and aggression is mixed and comes from only two recent studies. Wilson et al. (2010) found no relationship between signaling effort and aggression in domesticated European house crickets (*Acheta domesticus*). Similarly, Bertram and Rook (2012) found no relationship between signaling effort and aggression in laboratory-reared Jamaican field crickets (*Gryllus assimilis*). However, Bertram and Rook (2012) found a positive relationship between fine-scale components of signaling (such as signal amplitude and frequency) and aggression in laboratory-reared *G. assimilis* males. Because these studies reveal inconsistent patterns between signaling and aggression, there is a need to examine this relationship in other species. Further, given that previous studies were performed on domesticated and laboratory-reared individuals, there is an even stronger need to examine this relationship in field-captured individuals to determine whether relationships occur in nature.

In crickets, both signaling and fighting are important aspects in determining which males will be successful in mating. Male crickets signal acoustically to attract females and repel rival males (Alexander 1961). They rub their raised forewings together; each closing stroke produces a pulse of sound, and pulses are concatenated into chirps (Pfau and Koch 1994). Females use the acoustic properties of the male's long-distance signal to distinguish between potential mates. Female crickets tend to prefer males who invest the most effort into acoustic signaling. For example, female *Teleogryllus commodus* prefer males that signal most often (Hunt et al. 2004). In several cricket species, males that signal most through the night tend to mate most often (Cade and Cade 1992; Rodríguez-Muñoz et al. 2010). Signaling requires a territory, and males frequently compete for territorial signaling sites and access to females using discrete agonistic displays (fights/contests; Alexander 1961; Hack 1997; Hofmann and Schildberger 2001; Jang et al. 2008; Bertram et al. 2011). Winning contests increases male mating success via male–male competition and possibly through female choice favoring dominant males (Simmons 1986). Females of many animal species select dominant males as mates (fish, Doutrelant and McGregor 2000; birds, Mennill et al. 2002; e.g., crustaceans, Aquiloni and Gherardi 2010), and thus, fighting ability can directly influence reproductive success.

Our study had three goals: to investigate the relationship between signaling and aggression, to investigate the relationship between body condition and aggression, and to investigate the effect of fighting experience on subsequent signaling behavior. First, we addressed the question of

whether high-effort signalers are also highly aggressive in male–male contests or whether there is a trade-off between mate attraction ability and fighting ability. Understanding how sexual traits are related can reveal whether genetic quality or trade-offs prevail in the allocation of energy to sexual behaviors (Andersson and Simmons 2006). Because both mate attraction signaling and fighting are energetically costly (Hack 1997, 1998), males may be limited in their allocation of resources to each type of behavior. Using wild-caught and laboratory-reared spring field crickets (*G. veletis*), we quantified male signaling behavior on nights before and after they participated in staged aggressive contests to investigate the relationship between signaling effort and aggressiveness. We predicted that signaling would be an honest indicator of fighting ability, such that males that signaled with high effort would also display high levels of aggression during male–male contests.

Sexual signals are predicted to exhibit condition-dependent expression (genetic capture hypothesis; Rowe and Houle 1996) whereby males in good condition are able to simultaneously maximize multiple sexual signals. Given that aggressive behavior is costly (Hack 1997), males in good condition should have more energy to sustain agonistic displays and, therefore, experience higher success in contests than males in poor condition (Shackleton et al. 2005; Brown et al. 2006). A review of the sexual selection literature revealed that body size is the trait most likely to influence the outcome of both male–male competition and female mate choice (Hunt et al. 2009). Studies in several cricket species have found that larger males and males in better body condition (e.g., males with higher size-corrected mass) typically win aggressive contests against smaller opponents (e.g., *A. domesticus*, Hack 1997; *G. pennsylvanicus*, Judge and Bonanno 2008), but other studies have found no relationship between size or condition and aggressiveness (e.g., *G. assimilis*, Bertram et al. 2011). Therefore, our second goal was to examine whether body condition is related to aggressive behavior in *G. veletis*. We predicted that body condition would be related to aggressive behavior, such that males in good condition would display higher levels of aggression, due to increased resource-holding potential, compared to males in poor condition.

Finally, we compared signaling behavior before and after aggressive contests to determine whether contest outcome affects the signaling behavior of winners and losers differently. Biogenic amines, such as serotonin and dopamine, have been shown to play a role in aggressive behavior in invertebrates (e.g., Adamo et al. 1995). A recent study in *G. bimaculatus* found that the experience of winning a contest leads to an increase in motivation via the octopaminergic system, an invertebrate equivalent to the adrenergic system of vertebrates (Rillich and Stevenson 2011). We may thus expect differences in signaling behavior in winners and

losers following aggressive contests due to changes in internal chemical balances. We predicted that winners would increase signaling effort following their victory in an aggressive contest and, similarly, that losers would decrease signaling effort following their contest loss.

## Methods

### Experimental animals

We captured adult male and female field crickets (*G. veletis*) in Ottawa, ON, Canada (45°19' N, 75°40' W) in May and June 2008. Wild-captured males were held individually for 3 days prior to participating in agonistic trials to record their acoustic signals and also to minimize the effects of previous fighting or mating experience. We also used males from the first generation of laboratory-reared offspring. Late-instar nymph males were removed from the colony and checked daily for adult eclosion. Adult males were individually housed in circular, transparent plastic 540-mL containers. Crickets were provided with water and food (Harlan Teklad Laboratory Rodent Diet #8604: crude protein 24 %; crude fat 4 %; crude fiber 4.5 %) ad libitum and were held in a temperature-controlled room (30±2 °C).

### Acoustic recording

We placed males in an electronic acoustic recording system to record their long-distance mate attraction signaling (for details, see Bertram and Johnson 1998). The recording system determines when each male signals, how much time he spends signaling, and the duration of his signaling bouts. We recorded males for nine nights in total, three nights prior to their first contest, for each night immediately following the days they participated in a contests, and for the three nights following their last contest. Laboratory-reared males were placed in the recording system when they were 7 days post-eclosion and wild-captured males were recorded beginning the night after their capture. Each day, males were recorded for 18 h, from 1600 to 1000 hours. Recording was paused at 1000 hours to remove males for agonistic contests on the appropriate days and to replenish food and water.

### Agonistic contests

Males were weighed using a Denver Instruments Analytical Balance (Pinnacle Series Model PI-314; precision ±0.1 mg). Wild-caught males were weighed the morning after we captured them; laboratory-reared males were weighed on day 9 post-imaginal molt. Males were weight-matched for contests so there was no more than a 25 % difference in body mass between opponents. Opponents were weight-matched to

increase the probability that they would fight because several studies have shown that opponent size difference can influence aggression and contest outcome in crickets (e.g., Jang et al. 2008). Immediately following weighing, we placed a dot of colored nail polish on each male's pronotum to allow for identification during trials.

Each male participated in three contests, one per day for three consecutive days. Thirty-six wild-caught male *G. veletis* were paired in 54 experimental trials and 32 laboratory-reared males were paired in 48 trials. As part of a separate experiment, a third-party receiver (audience) was placed adjacent to the arena. The order of presentation of audience type (male, female, none) was systematically varied between males, and all males participated in one contest per audience treatment. Because we used aggression scores for all three contests for each male (see the "Statistical methods" section), we did not include audience type in our statistical models.

Agonistic trials were conducted in a small Plexiglas arena (15 cm  $L \times$  15 cm  $W \times$  21 cm  $H$ ) with two compartments separated by a removable divider and a sand-covered floor. All trials were filmed from above using a color video camera (Canon Vixia HG10) mounted on a tripod. One male was placed on each side of the divider and given 2 min to acclimatize to the arena and to have the opportunity to detect the audience. The divider was then removed, allowing the males to come into contact. Because agonistic behaviors are initiated after body contact (Jang et al. 2008), we defined a "contest" as the period of time from when males first came into body contact through to the establishment of clear dominance. Winners are easily identified because they typically chase the loser and often perform post-conflict victory displays (judders/body jerks and aggressive stridulations; Bertram et al. 2010; Logue et al. 2010), while losers retreat upon further contact (Alexander 1961; Hofmann and Schildberger 2001; Judge and Bonanno 2008; Bertram et al. 2010). We defined the end of the contest operationally as when one individual retreated in two consecutive encounters because we observed instances of dominance reversals in successive encounters in several contests. Cricket contests are typically comprised of short bursts of combat (termed "encounters") followed by longer periods of relative inactivity (Hack 1997). Thus, a trial was the entire observation period, a contest was the period within a trial in which the crickets were interacting and performing agonistic behaviors, and most contests were comprised of several agonistic encounters before clear dominance was established. Trials were terminated after the conclusion of the contest: once clear dominance was established between males, fighting had ceased, and all post-conflict displays had been completed. Once a trial was completed, the walls of the arena were wiped with 95 % ethyl alcohol and the sand raked to minimize the chance of contact pheromones affecting future contests (Judge and Bonanno 2008).

We conducted agonistic trials between 1000 and 1200 hours. Acoustic signaling and mating activity have been shown to peak at and after dawn in several cricket species, including *G. veletis* (French and Cade 1987), and thus the morning represents a time of day when motivation to fight is expected to be high. The duration and frequency of all agonistic behaviors were scored for each individual by replaying the videos in slow motion on a monitor. Our scale of aggressive behaviors ranged from 0 to 4: withdraw=0; antennal fencing=1; kick=2; mandible spread, chase, mandible engagement, or bite=3; and grapple=4 (Jang et al. 2008; Bertram et al. 2010, 2011).

For each male, we quantified total aggression score (Bertram et al. 2010, 2011) for each trial. We calculated the time each male spent performing various aggressive acts and then multiplied the aggression score for each behavior by the total number of seconds that behavior was performed, resulting in weighted aggression scores for each act. These weighted aggression scores were then summed across all behaviors each individual performed in a contest, resulting in a total aggression score for each male for each trial. To calculate aggression intensity score, the metric of aggression we used for analyses, we divided total aggression scores by the contest duration to account for variable contest duration (Bertram et al. 2010, 2011).

#### Body size measures

In addition to weighing males before contests, we measured head width, pronotum length, and pronotum width for each cricket following natural death. Measurements were taken using a Zeiss Axio Observer inverted dissecting microscope and highly magnified photographs (AxioVision v4.8, Carl Zeiss, Jena, Germany; magnification approximately  $\times 8.5$ , resolution  $\sim 1.60 \mu\text{m}$ ).

#### Statistical methods

We assessed within-individual variation in signaling and aggression scores by quantifying the repeatability ( $r$ ) using intraclass correlation coefficients following Falconer and Mackay (1996). Repeatability scores were calculated from the mean square values generated by ANOVA with individual as the predictor variable. Repeatability scores above 0.50 were considered high (Boake 1989).

We used linear mixed models (restricted maximum likelihood) to examine whether aggression was related to acoustic mate attraction signaling metrics, whether the males were wild-captured or laboratory-reared, male body size, and/or male body condition. Due to colinearity of the signaling variables and the body size metrics, we used principle components analysis (PCA) to reduce the number of factors in our models (Table 1). Because the aggression intensity scores of

**Table 1** PCA results for signaling and body size metrics

PCA	PC	Eigenvalue	Percent variance explained	Factors	Eigenvector
Signaling	PC1	2.04	56	Bout duration	0.98
				Time spent signaling	0.85
	PC2	0.82	39	Number of bouts	0.14
				Number of bouts	0.98
				Time spent signaling	0.45
				Bout duration	0.02
Body size	PC1	3.52	88	Mass	0.51
				Head width	0.50
				Pronotum length	0.50
				Pronotum width	0.50

opponent males were positively correlated (Pearson's  $r=0.44$ ,  $P<0.001$ ,  $N=80$ ), we ran models separately for winners and losers. We included the signaling metrics for the nights immediately preceding contest days and the three aggression intensity values (one per contest per male) for each male. Therefore, we included individual as a random effect in our models to account for multiple values per male.

Using matched-pairs analyses, we examined whether signaling parameters changed from the night before males first fought to the night after their first contest and whether this difference was influenced by whether the males won or lost their contest. We performed statistical analyses in JMP v9.0.2 (SAS, Cary, NC, USA). Data are presented as the mean  $\pm$  standard error.

#### Results

Over the course of the experiment, males signaled acoustically for  $60.14 \pm 3.45$  min per night, with an average of  $11.95 \pm 0.47$  signaling bouts per night and average signaling bout duration of  $4.42 \pm 0.30$  min. Three males never signaled, and the three highest effort signalers spent more than 5 h per night signaling. Descriptive statistics are presented in Table 2. Signaling PC scores were highly repeatable within individuals ( $r=0.62$ ).

Males displayed aggressive behavior in 78 % of trials. Contests averaged  $181.7 \pm 14.5$  s in duration and males spent  $87.0 \pm 9.8$  s performing aggressive behaviors during contests (Table 2). Unsurprisingly, winners consistently had higher aggression intensity scores than losers ( $1.46 \pm 0.16$  and  $0.63 \pm 0.09$ , respectively). Wild-captured males had higher aggression intensity scores than laboratory-reared males

**Table 2** Metrics of signaling effort and aggressive behavior

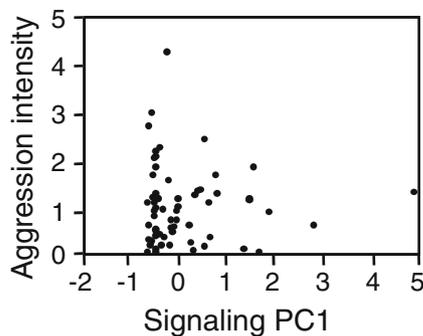
Behavioral parameter	Mean±SE	Median	Minimum	Maximum
Time spent signaling (min)	60.14±3.45	24.88	0	539.97
Number of signaling bouts	11.95±0.47	9	0	77
Signaling bout duration (min)	4.42±0.30	2.18	0	94.95
Total aggression score	152.3±20.74	41.5	0	2,227
Time spent performing aggressive behaviors (s)	87.0±9.80	25	0	821
Aggression intensity score (adjusted for variable contest duration)	0.82±0.084	0.32	0	8.83

Signaling was recorded for nine nights immediately following capture for wild-captured males, and for days 7–15 post-eclosion for laboratory-reared males. Males were acoustically monitored for 18 h/day (1600–0400 hours), and aggressive behavior was scored for three contests per male conducted on three consecutive days

(1.07±0.12 and 0.49±0.13, respectively). Aggression intensity scores had low repeatability within males across contests ( $r=0.15$ ).

Our models revealed that aggression scores were not related to signaling scores, male body size, or condition (Fig. 1; Table 3; winners:  $r_{\text{adj}}^2 = 0.81$ ,  $N=50$ ; losers:  $r_{\text{adj}}^2 = 0.25$ ,  $N=50$ ). However, for males that won contests, wild-captured individuals were more aggressive than laboratory-reared individuals (Table 3). Because of the observed difference in aggression between wild-captured and laboratory-reared males, we ran post hoc exploratory analyses separated by opponent (winner/loser) and rearing environment (wild-captured/laboratory-reared). Models separated by rearing environment produced results consistent with the pooled results above; for wild-captured and laboratory-reared winners and losers, aggression scores were unrelated to signaling scores, body size, and condition (all  $P \geq 0.13$ ). For visualization purposes, we plot the relationships between individual signaling parameters and aggression intensity scores in Fig. 2.

We found that time spent signaling did not change from the night before fighting to the night after fighting and was not influenced by whether males won or lost their contest (Fig. 3; matched-pairs  $t$  test:  $t=1.49$ ,  $P=0.14$ ,  $df=53$ ;



**Fig. 1** We found no relationship between male signaling behavior and aggressive behavior in *G. veletis*. This plot shows the mean signaling PC1 scores for the three nights before males fought and mean aggression intensity scores for each male

winner/loser:  $F=0.009$ ,  $P=0.92$ ). Similarly, there were no significant differences in the number of signaling bouts (matched-pairs  $t$  test:  $t=-0.31$ ,  $P=0.76$ ,  $df=53$ ; winner/loser:  $F=0.57$ ,  $P=0.45$ ) nor signaling bout duration (matched-pairs  $t$  test:  $t=1.53$ ,  $P=0.13$ ,  $df=53$ ; winner/loser:  $F=0.016$ ,  $P=0.90$ ).

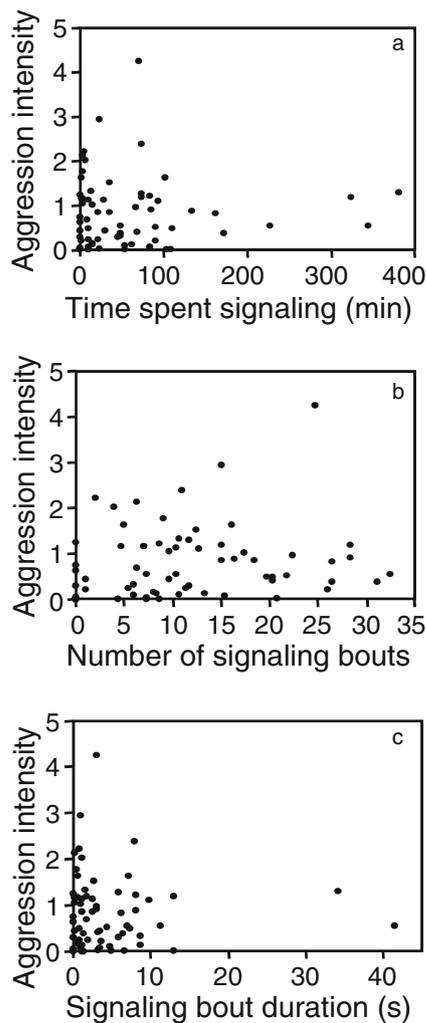
## Discussion

Our results indicate that signaling effort is not related to aggressive behavior in spring field crickets. We found neither a positive relationship, which would indicate an honest signaling scenario (Zahavi 1975, 1977), nor a negative relationship, which would indicate a potential trade-off between investment in signaling and aggression. Our results are consistent with those of Wilson et al. (2010) and Bertram and Rook (2012) that report no relationship between signaling effort and aggression in European house crickets (*A. domesticus*) and Jamaican field crickets (*G. assimilis*),

**Table 3** Results of general linear models reveal no relationships between aggressiveness and signaling effort, body size, or condition in *G. veletis*

Opponent	$r_{\text{adj}}^2$	Effects	Coefficient	$F$	$P$
Winners	0.81	Rearing environment	0.47	5.28	0.03
		Signaling PC1	0.27	2.48	0.12
		Body condition	-0.002	0.10	0.76
		Body size PC1	0.019	0.03	0.86
		Signaling PC2	0.021	0.02	0.90
Losers	0.25	Signaling PC1	-0.21	0.64	0.43
		Body condition	-0.003	0.44	0.51
		Rearing environment	-0.056	0.13	0.72
		Signaling PC2	-0.047	0.09	0.76
		Body size PC1	-0.006	0.006	0.94

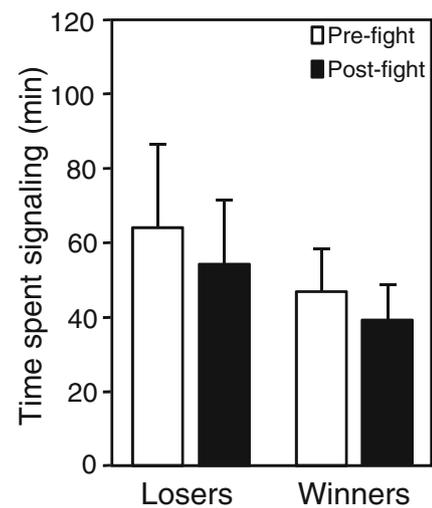
Rearing environment was significant in explaining variation in aggressive behavior in winners only; wild-captured males were more aggressive than laboratory-reared males



**Fig. 2** The lack of relationships between aggression intensity scores and individual signaling parameters: **a** mean daily time spent signaling, **b** mean daily number of signaling bouts, **c** mean length of signaling bouts

respectively. Together, these findings suggest that signaling effort is not indicative of aggressive behavior in crickets.

In our examination of signaling, we only quantified gross temporal aspects of acoustic signaling (total time spent signaling, number of bouts, bout duration) due to our recording system technology that limited our investigation to these aspects of signaling effort. It is possible that fine-scale aspects of the signals, including temporal and frequency characteristics, may contain information about fighting ability. Bertram and Rook (2012) revealed a positive relationship between the fine-scale components of signals and aggression in *G. assimilis*. Male *G. assimilis* that produce more attractive, higher effort signals (e.g., with more pulses per chirp, lower carrier frequency, and louder chirps) are more aggressive in male–male contests (Bertram and Rook 2012). To date, this is the only study to explore the relationship between fine-scale signal components and aggression



**Fig. 3** Neither losers nor winners changed their signaling behavior after participating in an aggressive contest. Values represent the total time spent signaling (mean±SE) for the nights immediately preceding and following the first day of aggressive contests

in crickets. Future work is required to determine if Bertram and Rook's finding is indicative of a general pattern in crickets or whether the relationship varies between species.

A second avenue for future research is to examine the signals produced immediately prior to agonistic interactions to address whether cricket acoustic signals communicate aggressive intent. This is an exciting and growing area of current research in animal behavior (Searcy and Beecher 2009; van Staaden et al. 2011), and studies of multiple signaling systems across taxa will improve our understanding of the functions of agonistic signals. For example, it is possible that features of aggressive songs produced immediately prior to an aggressive contest, such as the number of songs, the fine-scale components of the songs (Wagner 1992), or the song amplitude (Hof and Hazlett 2010), predict a male's aggressiveness in crickets.

The results of our repeatability analyses reveal that, while signaling behavior is highly repeatable within individuals, aggressive behavior is not. Our finding lies in direct contrast to a meta-analysis of the repeatability of various animal behaviors that concluded that aggression is one of the most repeatable behaviors for individuals across species (Bell et al. 2009). Since repeatability of aggression was low in our study, the lack of predictive relationship between signaling effort and aggression is perhaps unsurprising. Behaviors that are influenced by energy stores or the social environment may be relatively variable compared to behaviors under morphological or physiological constraint (Bell et al. 2009). In crickets, Briffa (2008) found that male *A. domesticus* that won contests had higher muscular glucose levels than losers, and a recent study revealed that male *G. veletis* display different levels of aggressive behavior in different social environments (Fitzsimmons and Bertram, in review).

Thus, aggressive behavior may be phenotypically plastic and highly variable within individuals, depending largely on both intrinsic and external factors. In order to estimate a more controlled metric of aggression, we suggest that future studies consider using techniques that remove confounding effects, such as opponent size, condition, and behavior, perhaps by assessing male aggression in simulated contests using a mirror instead of an actual opponent (e.g., Desjardins and Fernald 2010).

Our finding that winners and losers did not change their signaling behavior when comparing the night before they fought to the night after their first contest is also perhaps unsurprising in light of the low repeatability of aggression scores and the high repeatability of signaling scores. Further, we compared total signaling behavior over an 18-h period before and after contests, whereas a winner or loser effect may only be apparent on a much shorter time scale. For example, winner effects in *G. bimaculatus* disappear after 20 min (Rillich and Stevenson 2011), and both winner and loser effects last only an hour or two in jumping spiders (*Phidippus clarus*; Kasumovic et al. 2010). Traditionally, the winner and loser effects that are studied after aggressive contests are on subsequent aggressive behavior, but we predicted that an aggressive experience might also have effects on subsequent signaling behavior. In future studies, we will examine the signaling behavior of contest participants, including metrics of both signaling effort and fine-scale properties of signals, immediately following aggressive contests to examine whether there is a short-term winner or loser effect on signaling behavior.

The “aggressive songs” of crickets are produced prior to and throughout agonistic contests, and recently, Logue et al. (2010) revealed that the use of signals during agonistic interactions mitigates the costs of fighting. We investigated a separate acoustic signal, the long-distance mate attraction signal, but it is possible that aggressive songs, which are used only in the context of male–male contests, are more relevant to the question of whether the signals contain information about fighting ability or aggressive intent. Brown et al. (2006) studied aggressive songs in *A. domesticus* and found that temporal aspects of songs were indicative of male body size and that male size affected the intensity and outcome of contests. Our result that body condition was not related to aggression lies in contrast to the majority of studies in crickets that show a positive relationship between body condition and aggression (e.g., *A. domesticus*, Hack 1997; *G. pennsylvanicus*, Judge and Bonanno 2008). However, the evidence is certainly not unequivocal on this relationship; several other studies have found no relationship between size or condition and aggressiveness (e.g., *G. assimilis*, Bertram et al. 2011). Similarly, the evidence for a relationship between male size or condition and signaling effort is mixed. In a previous study of *G. veletis*, Fitzsimmons and Bertram (2011) found that neither

male size nor condition influenced the fine-scale components of signaling or signaling effort, while Bertram and Rook (2012) and Judge et al. (2008) found that males in good condition (higher residual mass and larger males raised on a high-quality diet, respectively) signaled with higher effort than males in poor condition in *G. assimilis* and *G. pennsylvanicus*. In sum and in contrast to our prediction, it appears that body condition is not related to aggressive behavior (present study) or signaling behavior (Fitzsimmons and Bertram 2011) in spring field crickets. Long-distance acoustic signaling and aggressive behavior appear to be independent of one another in spring field crickets, perhaps serving different functions in the two arenas of precopulatory sexual selection, female attraction and male–male competition.

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