

Male crickets adjust their aggressive behavior when a female is present



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ABSTRACT

Communication in nature often occurs within a broad social network, as signals can be perceived by other individuals beyond the primary intended receiver. Because signals often contain information about the signaller's quality, receivers other than the primary intended receiver may use this information in future interactions with the signaller. As a result, individuals who adjust their behavior depending on who is present may experience a selective advantage. The social environment can therefore have an important influence on the evolution of communication signals. We examined how the presence of a female audience influenced male aggressive behavior and post-contest victory displays in the Jamaican field cricket, *Gryllus assimilis*. We found a significant effect of female audience on aggressive interactions. When there was a female audience present, males were more likely to initiate and escalate fights, but they spent less time producing victory displays, compared to when there was no audience present. Our experiment suggests that the social environment is important in shaping the behavior of individuals during aggressive interactions.

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1. Introduction

Communication signals are used to convey information between signallers and receivers (reviewed in Rendall et al., 2009). Until recently, communication was often interpreted within a dyadic framework consisting of the lone signaller and the primary intended receiver. However, in nature, signals often travel further than the spacing between the signaller and the primary intended receiver, allowing for the signals to reach other potential receivers (also known as additional receivers, bystanders, audience members, and individuals other than the primary target; McGregor, 2005; Matos and Schlupp, 2005). Even though other potential receivers are not directly involved in the communication, Matos and Schlupp (2005) argue that the costs and benefits of communication must account for their presence. McGregor (2005) therefore proposes that communication should be interpreted as occurring within a network framework instead of within a dyadic framework. A network framework allows researchers to determine whether other potential receivers use information extracted from intercepted signals to inform them about the social environment,

including future potential encounters with the signaller (Peake, 2005).

When other potential receivers (audience members) are present, signallers often intentionally alter their behavior to control the information they transmit into the network, a behavioral response known as an audience effect (Desjardins et al., 2012; Matos and Schlupp, 2005; Ung et al., 2011). Audience effects have been documented in multiple taxa for multiple behaviors. For instance, male vervet monkeys (*Cercopithecus aethiops*) are more affectionate towards infants when the mother is in the vicinity (Hector et al., 1989), and male canaries (*Serinus canaria*) are less likely to pursue extra-pair courtship and copulations when their mates can see them (Ung et al., 2011). These changes in signaller behavior may confer a reproductive advantage by communicating higher quality to the nearby audience members.

Several studies reveal that the presence of an audience can also impact the signaller's aggressive behavior. For example, male cichlids (*Astatotilapia burtoni*) are less aggressive when a more dominant male is nearby, possibly to reduce the likelihood of a dominant audience member perceiving the signallers as threats (Desjardins et al., 2012). Further, male Siamese fighting fish (*Betta splendens*) reduce their aggressive behaviors and increase behaviors used in communication with both sexes when a female is present, possibly because females place importance on non-aggressive communication cues when assessing mate quality

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(Doutrelant et al., 2001). Given aggressive interactions have the potential to impact fitness, it is important to elucidate how social factors influence aggressive contest outcome.

Here we investigate how other potential receivers (audience members) impact aggression in a field cricket. We focus on field crickets because published studies of audience effects on cricket aggression are relatively rare despite the important effects that audiences impose on the signaling strategies of individuals. Further, the handful of published studies on audience effects and cricket aggression reveal conflicting results. For example, male *Gryllus veletis* (Fitzsimmons and Bertram, 2013) and *Gryllus bimaculatus* (Tachon et al., 1999) are more aggressive in the presence of a female, however, Judge et al. (2010) found no evidence of aggressive escalation in *Gryllus pennsylvanicus* when there was a female present. These studies were conducted using different experimental designs making it problematic to tease apart the impact of the mere presence of an audience. While Fitzsimmons and Bertram (2013) quantified aggression of virgin males with a female audience that the males could see but not touch, Tachon et al. (1999) quantified male aggression after introducing the female directly into the fighting arena and allowing for male–female interactions. Conversely, Judge et al. (2010) allowed one of the two males to mate or almost mate (researchers interrupted spermatophore transfer) and then observed how aggressive behavior was influenced with and without introducing the female directly into the fighting arena. It is time to discern the importance of female audience presence on aggression without the potential interacting effects of mating status and male–female interactions.

Cricket fights often include aggressive song (Alexander, 1962), and the function of aggressive song has been intensely debated (Logue et al., 2010). For example, aggressive songs are thought to be associated with dominance because dominant males stridulate more frequently than subordinates (Alexander, 1967). Aggressive songs are also thought to be associated with stimulating aggressive behavior because males can be induced to fight more easily when tactile stimulation is accompanied by aggressive song (Alexander, 1967). Conversely, aggressive songs may be associated with inhibiting aggressive behavior because fights among deaf males are more aggressive than fights among males that can hear and losers that are subsequently surgically deafened tend to dominate over previous winners when re-matched (Phillips and Konishi, 1973). In addition, fights among surgically silenced males are more aggressive than fights among males that can sing (Logue et al., 2010). Aggressive songs may also be associated with “victory” displays (a triumphant display performed by the winner at the conclusion of an aggressive contest; Bower, 2005), because males are more likely to produce an aggressive song after their opponent’s retreat than after their own retreat (Logue et al., 2010). Here we call aggressive song a victory display, but recognize that for the aforementioned reasons it could also be intertwined with inhibition and dominance.

The two main hypotheses proposed to explain victory displays are browbeating and advertising (Bower, 2005; Mesterton-Gibbons and Sherratt, 2006; Sherratt and Mesterton-Gibbons, 2013). Browbeating proposes that the winner directs the victory display towards the loser to reinforce dominance and discourage further aggression. Advertising proposes that the victory signals work within the network framework to communicate the win to potential mates or nearby rivals (Bower, 2005; Mesterton-Gibbons and Sherratt, 2006; Sherratt and Mesterton-Gibbons, 2013). In an experiment with silenced and song-capable males, Logue et al. (2010) revealed that aggressive song reduces fight intensity. Their findings suggest that aggressive songs are directed towards the opponent and function in browbeating. Conversely, in an experiment with audience members, Fitzsimmons and Bertram (2013) revealed that males produce more aggressive songs in the presence of a male audience than a female audience or no audience.

Their findings suggest that aggressive songs are directed towards other potential receivers (the male audience members that have the potential to be future opponents) and function in advertisement. Given only one of these studies conducted cricket fights with other potential receiver audience members as a treatment, our research explores how cricket aggression and victory displays are influenced by audience presence.

Here we used the relatively understudied Jamaican Field cricket, *Gryllus assimilis*, to stage aggressive contests in the presence of either one female audience member or no audience as a control. We hypothesized that female audience effects would occur. Since females of many taxa mate preferentially with dominant males (Otter and Ratcliffe, 2005), and two of three cricket studies show enhanced aggression (Fitzsimmons and Bertram, 2013; Tachon et al., 1999; but not Judge et al., 2010), we predicted that male *G. assimilis* would show elevated aggressive interactions when female audience members were present. Given the multiple possible functions of aggressive song and the fact that *G. veletis* only increased their aggressive songs when in front of a male audience but not a female audience, we refrained from making directional predictions about the effect of female audience on male victory displays. We also explored whether audience presence might influence male behavior by addressing whether female weight and time spent oriented towards the fight influenced male aggression and victory displays.

2. Methods

2.1. Cricket rearing

Laboratory-reared Jamaican field crickets (*G. assimilis*) were descendants (~18 generations) from wild caught individuals that were captured between September 15th and 24th 2008 around Smithville, Texas (latitude 30°0′26″N, longitude 97°9′18″W). We did not require specific permits for collecting invertebrates because these crickets are neither endangered nor protected. We imported adult crickets and eggs to our laboratory (Canadian Food Inspection Agency permit # 2007-03130). Our greenhouse facilities are Plant Pest Containment Level 1 certified (Canadian Food Inspection Agency permit # P-2012-03836). Our study was conducted in accordance with the guidelines of the Canadian Council on Animal Care.

Although not previously reported from Smithville, Texas, *G. assimilis* have been expanding their range in the USA since at least the 1940s (Alexander and Walker, 1962). *G. assimilis* was first identified in Florida in 1941 and has since become extremely abundant in southern Florida (Alexander and Walker, 1962). Since the 1940s, *G. assimilis* has expanded its range into Texas, but was only thought to occur in coastal Texas with one voucher specimen in central Texas (Walker, 2011; Weissman et al., 2009). However, members of our research team observed thousands of *G. assimilis* flying at lights around Smithville, Texas in 2007, 2009 and 2014. We identified this species as *G. assimilis* using distinctive morphological (narrow head, dense brown pubescence on the pronotum, Y-shaped ecdysial suture, lighter coloration than other Texas field crickets, and long-wings) and mate attraction signal features (average 8 pulses/chirp, faster pulse rate in the beginning of the chirp than the end, and extremely long interchirp interval) (Walker, 2011). We also digitized male long distance mate attraction signals and sent them, along with several individuals to D.B Weissman in August 2011; Weissman confirmed the mate attraction signals and morphology both conformed to *G. assimilis*.

We housed juvenile crickets in communal rearing bins in a greenhouse with a controlled temperature of $25 \pm 2^\circ\text{C}$ and a 14 h light: 10 h dark cycle. We provided crickets with *ad libitum* water

(small glass containers filled with water and capped with scrunched up paper towel), food (ground Harlan Teklad Laboratory Rodent Diet #8604M, 24% crude protein, 4% crude fat, 4.5% crude fibre, Indianapolis, Indiana, USA), and shelters made from cardboard egg cartons.

We collected adult crickets on the day of their last eclosion (imaginal moult) and weighed each individual to the closest 0.1 mg using a Denver Instruments analytical balance (Pinnacle Series model PI-314, Fisher Scientific, Ottawa, Ontario, Canada). We then placed each adult into an individual clear plastic container (540 ml) with a screened lid and provided it with *ad libitum* food, water in a gravel cup, and a ¼ piece of a scrunched up paper towel as shelter. Adult crickets were housed individually until trials were run to ensure virginity and to prime males for fights (Stevenson and Rillich, 2013); while housed individually, males and females could still see and hear other individuals.

2.2. Aggression trials

On day 11 post-imaginal moult, we re-weighed all crickets. We weight-matched males such that opponents body weights were within 25% of each other to increase the chance of fighting and to control for the effects of weight difference, which can affect contest behavior (*sensu* Jang et al., 2008). We then painted the pronotum of each opponent using different colored nail polish so we could individually identify the opponents during the aggression trials.

We conducted all aggression trials between 16:00–20:00 from October 29th to November 17th 2013 in a quiet room at $25.1 \pm 0.4^\circ\text{C}$. All aggression trials were conducted in a Plexiglas arena (15 cm L \times 15 cm W \times 21 cm H). We subdivided the container into three chambers separated by clear removable barriers. The transparent barrier separating the two males from the audience observation chamber was perforated to allow transmission of auditory, visual, and olfactory cues. The bottom of the arena was covered in white sand. We raked the sand after each trial and changed it after every tenth trial to reduce the effect of pheromones on later trials. We also cleaned the arena walls with 95% ethyl alcohol between trials. We placed the Plexiglas arena in a larger wooden box to reduce human observer interference and filmed all trials from above using a color video camera (Canon Vixia HG10, Mississauga, Ontario, Canada).

We fought males at 12 days post-imaginal moult. We conducted each trial with either one twelve-day-old female present in the audience observation chamber (female audience treatment), or with an empty audience observation chamber (control treatment). We randomly assigned each pair of male opponents to a trial type (female audience or no audience). Males and females participated in only one trial. We placed the two opponent male crickets in the main fight chamber of the Plexiglas arena, separating them with a non-perforated, transparent barrier and allowed these two males to acclimatize for 5 min. When females were present males sometimes antennated with them through the perforated barrier or produced long distance acoustic mate attraction signals, suggesting the males often detected the presence of the female. We then removed the barrier between male opponents and allowed the male crickets to interact for 10 min (trial period). Given agonistic behaviors start after body contact, we defined contest duration as the time from initial body contact until dominance was established (*sensu* Jang et al., 2008). Dominance was established when the opponent retreated twice consecutively; we used two consecutive retreats as a measure of dominance because dominance reversals can occur (*sensu* Bertram et al., 2011; Fitzsimmons and Bertram, 2012). Trials were stopped when dominance was established or at the 10 min mark, whichever came first. At the conclusion of trials, we euthanized (froze) crickets so they could be quantified for body size. We ran 31 trials with a female audience and 35 trials with no

audience (control trials). We ran more control trials than female audience trials because a subset of the opponents in the control trials did not fight.

2.3. Scoring trials

We scored trials by watching videos in real time using JWatcher (version 1.0, <http://www.jwatcher.ucla.edu/>). To ensure consistency, one observer scored all trials. To score the trials, we followed the approach detailed by Stevenson and Rillich (2012) and Bertram et al. (2011), which were adapted from Adamo and Hoy (1995). We gave behaviors a score on a scale from 0 to 5 based on their perceived level of aggression (Table 1). We quantified aggression for each individual for each trial using total aggression score (*sensu* Bertram et al., 2011). To measure total aggression score, we multiplied each behavior's aggression score by the total number of seconds it was performed during the contest and then summed these weighted aggression scores across all the behaviors each individual performed.

Victory displays included either body jerks (also known as judders or rock body displays) or body jerks coupled with aggressive song. Body jerks describe a cricket's intense whole body shaking forwards and backwards (Jang et al., 2008). Aggressive songs (also known as aggressive stridulations, signals, calls, or chirps) are short bursts of sharp brief chirps that are typically performed at higher frequencies and amplitudes than normal long distance mate attraction songs (Alexander, 1962; Huber et al., 1989). We quantified victory displays performed during the contest by summing the number of seconds they occurred. Victory displays were not given an aggressive score.

We quantified the amount of time females spent oriented towards the males during the ten-minute trial period by identifying the angle the female was facing. We gave a female a score of 0° when her head was oriented directly toward the fight chamber and her sagittal axis was perpendicular to the wall that divides the audience observation chamber from the fight chamber; we gave a female a score of 90° when her sagittal axis was parallel to the wall that divides the audience observation chamber from the fight chamber; we gave a female a score of 180° when her head was oriented directly away from the fight chamber and her sagittal axis was perpendicular to the wall that divides the audience observation chamber from the fight chamber. We quantified total time spent oriented towards the males during the fight by determining the number of seconds each female spent with scores less than 90° .

2.4. Body size

We quantified male body size by taking pictures of the frozen crickets (dorsal side up) using a Mycro USB Microscope (EmCal Scientific Inc., San Diego, California) with a standard scale visible in each image. We used ImageJ (version 1.48, National Institutes of Health, <http://imagej.nih.gov/ij/>) to quantify three size measures from the pictures: pronotum length (maximal distance down the sagittal length of the pronotum), pronotum width (maximal measure transversely across the pronotum) and head width (maximal distance between the outer edges of the eyes). We then incorporated these measurements into principal component analysis in JMP (version 11.0.0, SAS, Cary, NC, USA) to get an overall measure of male body size. The first principal component (PC1) was a strong measure of overall size as it had an Eigenvalue greater than one, explained 87% of the variation, and all three measures were weighted equally.

Table 1

Cricket agonistic behaviors and their scores [adapted from Stevenson and Rillich (2012) and Bertram et al. (2011), which were adapted from Adamo and Hoy (1995)].

Aggressive behavior	Description	Score
No aggression	Not engaging in aggressive behavior	0
Withdraw	Moves away from opponent	0
Antennal fencing	Rapidly antennates opponent	1
Kick	Kicks leg towards opponent (contact unnecessary)	2
Unilateral mandible spreading	One hyperextends mandibles	3
Unilateral aggressive signalling	One signals aggressively	3
Chase	Runs after opponent	3
Bite	Pinches opponent with mandibles	3
Lunge	One lunges at opponent	3
Bilateral mandible spread	Both face each other and extend mandibles	4
Bilateral aggressive signalling	Both within close proximity and calling	4
Head butt	Both butt heads	4
Grappling	Both interlock mandibles while butting heads and push, pull, or flip their opponent	5

2.5. Statistical analysis

We ran all statistical analyses in JMP version 11.0.0 (SAS, Cary, NC, USA). We tested whether audience type (female or none) influenced the likelihood of a fight occurring, using a chi-square test. We used general linear models (GLM: standard least squares) to examine if audience effects existed for male aggression and victory displays. We excluded the trials where males did not fight from analyses, resulting in 30 trials for the female audience treatment and 28 trials for the no audience treatment. Explanatory variables were audience type, while covariates were average male size (averaged across each pair of opponents) and size difference of opponents (maximum–minimum size). To account for the fact that one male's aggression may influence their opponent's aggression, we averaged the total aggression scores of the two males (in the trial). To examine victory displays we used total time spent performing victory displays (body jerks alone or in conjunction with aggressive song) as our response variable. Similar to the aggression scores, the two males' time spent performing victory displays scores were averaged to give one victory score per trial. To examine whether audience effects influenced the relationship between victory displays and aggressive behavior, we used total time spent performing victory displays as our response variable, and total aggression score, audience type, and their interaction as explanatory variables. We also ran a GLM to determine if female weight and the time females spent oriented towards males influenced male aggression or victory displays in the treatment with a female audience. The response variables were the same as described above, while the explanatory variables were male size (averaged across the two male opponents), size difference between male opponents, female weight, and time females spent oriented towards males. All model residuals met parametric assumptions.

3. Results

Males fought in most trials that we conducted (58 of 66 = 88% of trials). In the eight trials that males did not fight, seven had no audience, revealing fights are more likely to occur when an audience is present than when no audience is present (97% versus 80%, respectively; Pearson $\chi^2 = 4.34$, $df = 1,66$, $R^2 = 0.10$; $p = 0.037$). Our GLM explained 12% of the variation in aggressive behavior and revealed that fights in the presence of a female audience were significantly more aggressive than fights with no audience (Table 2; Fig. 1). Average male size and size difference between the opponents did not significantly influence aggressive behavior.

Victory displays occurred in $\frac{3}{4}$ of trials with fights (44 of 58 = 76% of trials). While victory displays occurred more often in fights with no audience (82%) than they did in fights with an audience (67%), this difference was not statistically significant (Pearson $\chi^2 = 1.81$, $df = 1,58$, $R^2 = 0.02$, $p = 0.179$). Winners performed the vast major-

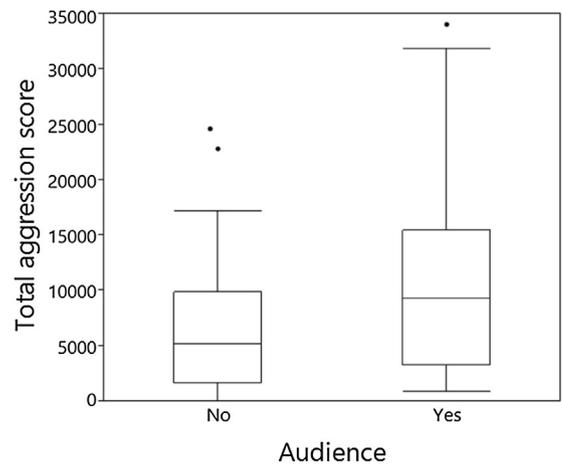


Fig. 1. Comparison of male total aggression scores during agonistic contests either in the presence of a female audience or no audience. The box represents the middle 50% of the scores (interquartile range), with the middle line representing the median. The whiskers are drawn to the furthest data point within 1.5 times of the interquartile range. The disconnected points are outliers that fall above the 1.5 times out of the interquartile range. Scores are significantly different between the treatment and control.

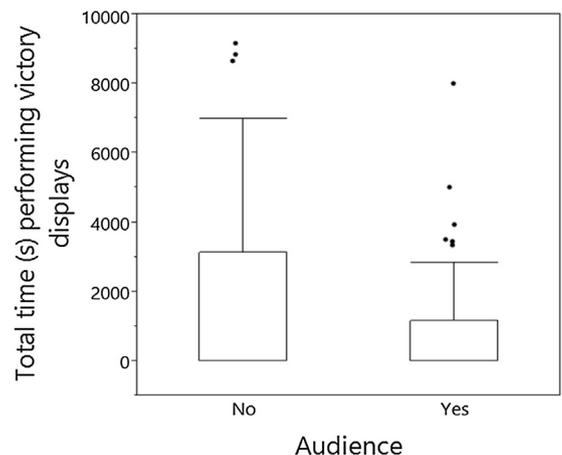


Fig. 2. Comparison of the total time spent performing victory displays between treatments. The box represents the middle 50% of the scores (interquartile range), with the middle line representing the median. The whiskers are drawn to the furthest data point within 1.5 times of the interquartile range. The disconnected points are outliers that fall above the 1.5 times out of the interquartile range.

ity of victory displays (41 of 45 = 91%), and losers only performed victory displays before the contest was concluded. Our model explained 24% of the variation in time spent performing victory displays and revealed that audience treatment, aggressive behav-

Table 2
GLM results analyzing the effect of audiences on male aggression and victory displays; significant results bolded.

Behavior	Source	R^2_{adj}	DF	Estimate	t	F	p
Total Aggression Score	Overall Model	0.12	3, 54			3.5	0.022
	Audience			-2224.05	-3.19	10.2	0.002
	Average male PC1 size			192.74	0.48	0.23	0.631
	Male PC1 size difference			523.29	0.52	0.27	0.608
Victory Display Time	Overall model	0.24	5,50			4.48	0.002
	Audience			592.94	3.58	12.81	0.001
	Average total aggression score			0.06	2.13	4.52	0.039
	Audience × average total aggression score			0.07	2.26	5.11	0.028
	Average male PC1 size			-129.64	-1.51	2.27	0.138
	Male PC1 size difference			294.07	1.37	1.88	0.177

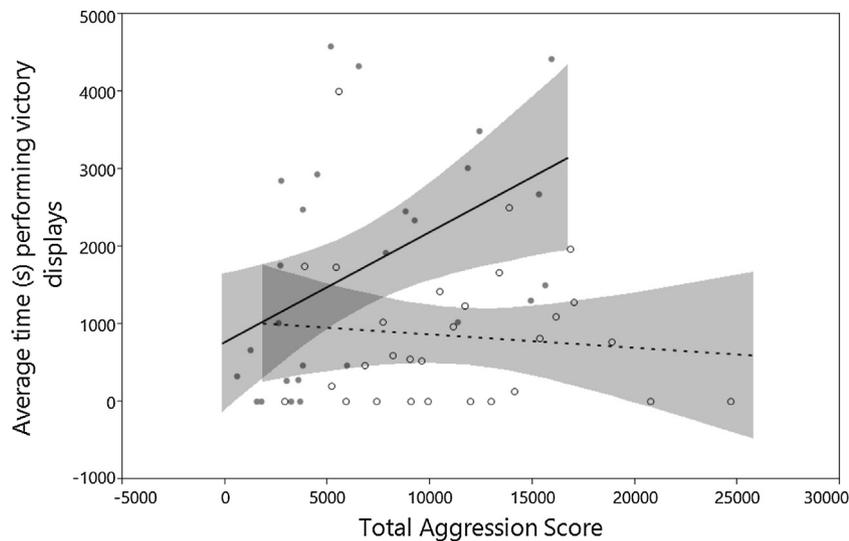


Fig. 3. Relationship between total time spent performing victory displays and aggression in the two treatments (female audience represented by a dashed line; no audience represented by a solid line). There was a significant interaction effect, revealing that victory displays increase with increasing aggression when there is no audience present; there was no relationship between victory displays and aggression when a female audience was present. Data from the female audience treatment is presented with open circles, while data from the no audience treatment is presented with solid circles. Grey shading represents confidence intervals.

ior, and the interaction between audience treatment and aggressive behavior were significant predictors. Males produced victory displays for less time when a female audience was present than when no audience was present (Table 2; Fig. 2). Further, males produced victory displays for more time when fights were more aggressive, provided there was no female audience member present (Table 2; Fig. 3). When there was a female audience member present, there was no relationship between time spent performing victory displays and male aggressive behavior (Table 2; Fig. 3). Average male size and the size difference between opponents did not influence time spent performing victory displays.

Neither male aggression nor victory displays were influenced by the amount of time females spent oriented towards the fight chamber (Table 3). Similarly, neither male aggression nor victory displays were influenced by female weight (Table 3). Average time spent performing victory displays in front of a female audience increased with increasing size discrepancies between male opponents (Table 3).

4. Discussion

Signals often travel further than the spacing between the signaller and the primary intended receiver, allowing for the signals to reach other potential receivers. Given the costs and benefits of signalling must account for the presence of these other potential receivers, communication should be interpreted as occurring within a network (Matos and Schlupp, 2005; McGregor, 2005). Our

study adds to the growing body of research suggesting other potential receivers impact behavior (Desjardins et al., 2012; Fitzsimmons and Bertram, 2013; Matos and Schlupp, 2005; Ung et al., 2011). Our data reveal that the presence of a female adjacent to the fight arena changed the dynamics of agonistic interactions between *G. assimilis* males: males were more aggressive but reduced the time spent producing victory displays when a female audience was present compared to when there was no audience present.

Aggression is only adaptive if the benefits of winning fights outweigh the costs, such as when the winner of aggressive interactions acquires resources after competition (Dabelsteen, 2005; Ficken et al., 1990; Grossman, 1980). Aggression can be both energetically costly and increase risk of injury. While the amount of energy required for aggressive interactions is unknown in *G. assimilis*, Hack (1997a) determined that aggressive interactions carry substantial energetic costs for crickets; male house crickets, *Acheta domesticus*, expend approximately eight times more energy when fighting than when resting. Since males in our study were significantly more likely to initiate fights in the presence of a female audience and their fights were significantly more aggressive, the potential payoff (potential to court the female) may be a valuable enough resource to outweigh their elevated energetic expenditure.

When one utilizes a dyadic framework perspective, the benefits of signalling can only come from the primary intended receiver's response (McGregor and Peake, 2000). With a network framework perspective, signalling benefits can also come from other potential receivers (Earley, 2010), as audience members can gather

Table 3
GLM results analyzing the effect of females on male aggression and victory displays; significant results bolded.

Behavior	Source	R ² _{adj}	DF	Estimate	t	F	p
Total Aggression Score	Overall model	−0.08	4, 25			0.47	0.758
	Average male PC1 size			665.34	1.05	1.11	0.303
	Male PC1 size difference			1112.20	0.71	0.50	0.484
	Female weight			5.31	0.55	0.30	0.588
	Time female spent oriented			4.64	0.60	0.36	0.553
Victory Display Time	Overall model	0.03	4, 24			1.19	0.340
	Average male PC1 size			−52.90	−0.51	0.26	0.614
	Male PC1 size difference			543.34	2.12	4.52	0.044
	Female weight			−0.02	−0.01	0.00	0.992
	Time female spent oriented			−1.20	−0.96	0.96	0.348

information about male quality and use this information to inform their future behavior (e.g., whether to mate or engage in an aggressive interaction; Otter and Ratcliffe, 2005). Females from many taxa prefer to mate with dominant males [Siamese fighting fish (*B. splendens*) (Doutrelant and McGregor, 2000), and Great Tits (*Parus major*) (Otter et al., 1999)], possibly because dominant males are of better quality (Qvarnström and Forsgren, 1998). In crickets it is unclear whether females prefer dominant males as mates. While Tachon et al. (1999) demonstrated that female *G. bimaculatus* prefer winners over losers, Shackleton et al. (2005) found no such preference in *Teleogryllus commodus*. If female *G. assimilis* prefer to mate with fight winners, males should be selected to elevate the energy they spend on aggression to increase their future mating opportunities when females are present.

Regardless of whether females prefer to mate with winners, female presence alone may be a valuable enough resource to outweigh the elevated energetic costs associated with escalating a fight. Given males fight over access to calling territories, males may be more motivated to fight for the territory if they perceive females adjacent to the fighting arena (Alexander, 1961). In support of the hypothesis that crickets dynamically adjust their aggressive behaviour to acquire limited resources, hungry male European field crickets have been shown to be more aggressive in the presence of food (Nosil 2002). Further, Judge et al. (2010) found no evidence of aggressive escalation in recently mated *G. pennsylvanicus* when there was a female present. To ascertain if elevated aggression results from selection by eavesdropping females and/or from limited resources, future research should examine if elevated aggression also occurs with different types of audiences (juvenile, adult male, adult female) and/or when males have been recently mated.

While our finding that the mere presence of a female elicits a more aggressive response is intriguing, the low effect size (12% of the variation was explained by our GLM) suggests aggression is also simultaneously influenced by other factors. Neither female size nor female orientation towards the fight explained variation in male aggression. Perhaps this should not come as a surprise, given males' attention would likely be drawn to their opponent as soon as the fight began. Other factors known to influence aggression in field cricket species include differences in social experience (DiRienzo et al., 2012; Nagamoto et al., 2005; Simmons, 1986; Tachon et al., 1999), mating experience (Judge et al., 2010), operational sex ratio (Souroukis and Cade, 1993), past fighting experience (Hofmann and Stevenson, 2000; Khazraie and Campan, 1999; Simmons, 1986), age (Dixon and Cade, 1986), weight (Hack, 1997b; Shackleton et al., 2005; Simmons, 1986), morphology (Judge and Bonanno, 2008), time of day (Dixon and Cade, 1986), and motivation to fight (Nosil, 2002; Rillich and Stevenson, 2011). Our study controlled for several but not all of these factors. Unexplained variation in aggression could have been driven by morphological differences

between opponents (Judge and Bonanno, 2008), experience as juveniles (DiRienzo et al., 2012), and motivation to fight (Rillich and Stevenson, 2011).

Male *G. assimilis* reduced the amount of time they spent performing victory displays in the presence of a female audience relative to the no-audience control. In a similar study on *G. veletis*, Fitzsimmons and Bertram (2013) revealed that males did not dynamically alter the amount of time they spent performing victory displays in the presence of a female audience relative to the no-audience control; however, when there was a male audience present, males dynamically increased their time spent performing victory displays relative to the no-audience control. While it is possible that males reduce their victory displays in the presence of a female audience because they have insufficient energy after the fight, support for this hypothesis is lacking given males in the no audience treatment increase time spent performing victory displays with escalating aggressive interactions. Alternatively, males may spend less time producing victory displays because they quickly refocus their attention on the female, shunting energy from the production of victory displays into energy for female attraction. When large asymmetries occurred between the fighting males, the relatively larger males may have had enough extra energy to signal both their dominance and their viability to both the rival male and the female audience members, and therefore spent more time producing victory displays.

Given winners were much more likely than losers to produce body jerks and aggressive song, and most body jerks and aggressive songs occurred at the conclusion of the fight, these behaviors appear to function as victory displays (Fitzsimmons and Bertram, 2013; Logue et al., 2010). The function of the victory displays appear to be largely directed towards the opponent, given time spent performing victory displays increased with increasing aggression in the control treatments (no audience present). Victory displays may also occasionally serve as signals to females about male viability, especially when the opponents are very asymmetrical in size. Together these findings suggest that victory displays function in browbeating. Caution is warranted, however, as our study did not test male audiences. Fitzsimmons and Bertram's (2013) study on *G. veletis* suggest that aggressive songs function in advertising to male audience members.

Our findings add to the growing number of studies revealing that male crickets increase aggression in the presence of females [*G. bimaculatus*: Simmons (1986); *G. veletis*: Fitzsimmons and Bertram (2013)]. Together with our findings, these studies suggest that crickets adjust their aggressive behavior based on their social environment. Given this, the social environment appears to be an important factor in shaping the evolution of aggressive signalling (Dzieweczynski, 2005). Researchers should, therefore, adopt a network perspective when studying communication.

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