Strutting their stuff: victory displays in the spring field cricket, *Gryllus veletis*

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Summary

Contest winners may perform victory displays at the conclusion of agonistic contests. Victory displays are hypothesized to function in browbeating or advertisement. To date, victory displays have received little attention. Following agonistic contests, several field cricket species produce aggressive songs and shake their body forwards and backwards (body jerks). We examined 20 agonistic contests between field-captured adult male spring field crickets, *Gryllus veletis*. We characterized the aggressive songs and body jerks that occurred both during and immediately following conflicts to evaluate whether these behaviours should be classified as victory displays. Aggressive songs and body jerks were observed throughout the contests, not just immediately following the conclusion of the fight. Winner aggressive song and body jerk rates were higher during the post-conflict period than during the fight period. Further, while both winners and losers performed aggressive songs and body jerks, winners performed them at five times the rate of the losers during the post-conflict period. We conclude that aggressive songs and body jerks should be considered victory displays, and that these victory displays may function as both browbeating and advertisement.

Keywords: *Gryllus veletis*, post conflict display, fight, rock body displays, judder, vibration, aggressive stridulation, aggression, contest.

Introduction

Research on animal communication has lead to great advances in our understanding of the evolution of signals associated with agonistic contests (Maynard Smith, 1982; Huntingford & Turner, 1987; Bradbury & Vehrencamp,

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1998; Johnstone, 2001). To date, however, there has been little research on the communication signals that occur upon the conclusion of agonistic contests (post-conflict signals) (Bower, 2005). What research has been done has focussed largely on birds. Examples of post-conflict displays in birds include: (1) the loud cackling and vigorous wing flapping displays of victorious mated pairs of greylag geese (*Anser anser*) following the male's agonistic encounter with a rival (the triumph ceremony; Heinroth, 1910), (2) the victorious duet produced by pairs of tropical boubous (*Laniarius aethiopicus*) after winning territorial disputes (Grafe & Bitz, 2004), (3) the victorious displays of lone male song sparrows (*Melospiza melodia*) that sing at elevated rates after winning agonistic contests (Bower, 2000) and (4) the loser displays of black-capped chickadees (*Poecile atricapillus*) that sing at elevated rates after losing agonistic contests (Lippold et al., 2008). Given post-conflict displays appear relatively common in nature, it is somewhat surprising that so few studies have focussed on how animals behave after agonistic contests (Bower, 2005). This is especially true given the significant consequences that post-conflict displays may have on receivers, regardless of whether they are participants in the agonistic contests or nearby observers. Determining the function of post-conflict signals has the potential to enhance our understanding of complexities associated with communication network interactions, especially if post-conflict displays reduce the costs of further contests between rivals.

Post-conflict displays may serve several possible functions. Post-conflict displays performed by the winner are often called 'victory displays' (e.g., Bradbury & Vehrencamp, 1998) and may function to reinforce the dominance of the winner, thereby decreasing the probability that the loser will initiate a future contest (browbeating rationale; Bower, 2005; Mesterton-Gibbons & Sherratt, 2006). Victory displays may also function to communicate the victory to nearby prospective mates or potential rivals (advertising rationale; Bower, 2005; Mersterton-Gibbons & Sherratt, 2006). Loser displays may function to prevent aggression from nearby individuals (loser rationale; Kazam & Aureli, 2005; Lippold et al., 2008). Conversely, post-conflict displays might have no function at all, resulting instead from the mechanisms that drive the aggressive contests such as releasing pent-up aggressive energy caused by an elevated hormonal state (null hormone release rationale; Bower, 2005).

Here we investigated two potential post-conflict displays in a field cricket: aggressive songs and body jerks. Male crickets frequently engage in agonistic contests to gain access to food, establish dominance and gain access to mate attraction territories (Alexander, 1961). Cricket agonistic contests are composed of a series of discrete and easily scored behaviours that increase in aggression and energy expenditure as the fight progresses (Alexander, 1961). Winners and losers can typically be clearly identified (Hofmann & Schildberger, 2001). Crickets often perform aggressive songs and body jerks following an agonistic conflict (Alexander, 1961; Jang et al., 2008; Logue et al., 2010). Both aggressive songs and body jerks are, therefore, thought to be post-conflict displays (Alexander, 1962; Jang et al., 2008; Logue et al., 2010). Aggressive songs (also known as aggressive stridulations, aggressive calls, or aggressive chirps) are brief bursts of sharp short chirps, performed at higher frequency and amplitude than normal calling song (Alexander, 1962; Huber et al., 1989). While the sensory modalities of aggressive songs clearly include visual and acoustic components, they may also include vibrational components (Kamper & Dambach, 1985). Body jerks (also known as rock body displays and judders) describe a cricket's intense whole body shaking rapidly back and forth (Jang et al., 2008). The sensory modalities of body jerks are less clear, but have the potential to be perceived by nearby individuals through vibrational and visual sensory modalities (Kamper & Dambach, 1985).

In nature, communication often occurs in the context of a communication network, with several signalers (males signaling to repel other males or attract mates) and receivers (potential mates and potential rival males) within range of one another (McGregor, 2005). This is the case in crickets where both agonistic encounters and acoustic mate attraction signalling occur in immediate proximity to each other and at relatively high densities (Alexander, 1961; Cade & Cade, 1992). Both male and female audiences may be common during field cricket agonistic contests. It is, thus, plausible that aggressive songs and body jerks could have any of the aforementioned functions for post-conflict displays (browbeating, advertising, loser and hormone release).

Aggressive songs and body jerks occur during agonistic encounters, not just following them. Further, both winners and losers have been observed to perform aggressive songs and body jerks. Alexander (1961, p. 135–136)

wrote "When either male stridulates during prolonged combat, the other usually stridulates immediately afterward... It is common for the subordinate male to stridulate once or twice during an intense encounter, then retreat, this followed by the dominant male stridulating several times". Jang et al. (2008) quantified this observation using a Markov Chain analysis. In a detailed review of aggression in several Eastern field cricket species, Jang et al. (2008) revealed that while aggressive songs and body jerks usually occur following a fight, they can also quickly lead to threat postures, mandible flares, chasing, biting, lunging and grappling. Logue et al. (2010) also confirmed that aggressive songs can be produced by both winners and losers and can lead to further conflicts in the oceanic field cricket, *Teleogryllus oceanicus*.

Given that aggressive songs and body jerks can be performed by both winners and losers, and during and after agonistic contests, the following questions must be addressed: Can behavioural displays that occur during, as well as after a conflict be considered to be post-conflict displays? If so, how should researchers quantify when a conflict ends and the post-conflict display begins? Further, under what contexts (if any) can a loser perform a post-conflict display and that display still be considered a victory display? Addressing these questions is a necessary first step towards understanding the function of post-conflict displays in crickets. We, therefore, provide the first formal quantification of aggressive songs and body jerks associated with agonistic conflicts between male spring field crickets, *Gryllus veletis*. We determine which individual (the winner or loser) produces more aggressive songs and body jerks. We also determine whether aggressive songs and body jerks occur more frequently during the conflict or during the post-conflict period. We then ascertain the factors contributing to the occurrence and rate of aggressive songs and body jerks. Our results suggest that both aggressive songs and body jerks should be considered to be post-conflict victory displays.

Materials and methods

Experimental animals

We captured adult male *G. veletis* in Ottawa, Ontario Canada (45°19′N, 75°40′W) in June, 2008. Because captured males were of unknown fighting status, they were held individually in a rearing room (controlled temperature

$25 \pm 2°C$) for three days prior to fighting to minimize the effects of previous fighting experience. Males were individually housed in circular, clear plastic containers (11 × 7 cm H). Crickets were provided with food ad libitum (powdered Harlan Teklad Rodent diet no. 8604) and water.

Agonistic contests

Agonistic contests were conducted in a small, sand-covered Plexiglas arena (15 × 15 × 21 cm H) with two compartments separated by a removable divider. All contests were filmed from above using a colour video camera (Canon HG10) mounted on a tripod. We covered the outside of the arena with white paper so that our presence did not disturb the crickets. We conducted trials between 1000 and 1200 h. We paired crickets for trials based on minimizing mass differences between opponents (males were weighed at least one day prior to the agonistic contest using a Denver Instruments balance Pinnacle Series model PI-314). We weight-matched opponents to increase the chance that they would fight because Jang et al. (2008) revealed that the difference in size between opponents was a critical factor influencing aggression and fight outcome in *G. pennsylvanicus*. Opponents were matched to within 25% of total body mass.

Forty individual male crickets were paired in 20 agonistic contests. Each cricket was used in only one contest, and was identified with a coloured marking painted on its pronotum with nail polish. Males were placed on each side of the divider and given 2 min to acclimatize to the arena. The divider was then removed allowing the males to come into contact. The timing, duration and frequency of all agonistic behaviours were scored for each individual by replaying the video in slow motion on a computer monitor. We quantified agonistic behaviour of the contest participants with a scoring system adapted from Hofmann & Schildberger (2001). Our scale of aggressive behaviours ranged from zero to six: 0, mutual avoidance; 1, pre-established dominance; 2, antennal fencing; 3, unilateral mandible spreading; 4, bilateral mandible spreading; 5, mandible engagement; 6, grappling or wrestling (Hofmann & Schildberger, 2001; Table 1). Once a clear winner and loser had emerged, the crickets were left in the arena for a few more minutes to allow us to record post-conflict displays. Trials were terminated once clear dominance was established between males, the fighting had ceased and all post-conflict displays had been completed. Once a trial was completed, the

Table 1. Agonistic behaviours and their intensity score value.

Behaviour	Description	Level of aggression
Mutual avoidance	No interaction between the opponents occur or they are immobile for more than 15 s	0
Pre-established dominance	One opponent has early dominance over the other	1
Antennal fencing	Crickets rapidly antennate the others antennae	2
Unilateral mandible spreading	One of the opponents hyper-extends its mandibles	3
Bilateral mandible spreading	Both opponents hyper-extend mandibles	4
Mandible engagement	Opponents lock and pinch each other with mandibles	5
Grapple/wrestling	Crickets butt heads and/or interlock mandibles and push or pull their opponent	6

Adapted from Hofmann & Schildberger (2001).

walls of the arena were wiped down with 95% ethyl alcohol, and the sand raked to minimize the chance of pheromones affecting future fights. Nineteen of twenty contests had a clear winner and loser (95%). One contest with continuous mutual male courtship was excluded from our analysis.

Because agonistic behaviours are initiated after body contact (Jang et al., 2008), the start of the contest was defined as the first body contact between the two males. The conclusion of the contest occurred when one individual retreated in two consecutive encounters. The contest duration was defined as the entire observation period, from the start of the contest to the termination of the observation period following the conclusion of the contest. We used physical engagement (except where noted) to subdivide the agonistic contest into fight periods and post-conflict periods. The cricket pair was defined as being in a fight period when they were physically engaged; once the pair were no longer physically engaged they were defined as being in a post-conflict period. Opponents who were engaged in a fight and then broke apart for no longer than 2 s before re-engaging in the fight were considered to be in one continual fighting period. By definition, antennal fencing, mandible engagement and grappling/wrestling require physical contact and, therefore, easily fall into the fight period. While physical contact is not necessarily required for unilateral or bilateral mandible spreading we considered individuals that were engaged in unilateral or bilateral mandible spreading to also be in the fight period.

Contest aggressiveness has historically been quantified by reporting the maximum level of aggression reached during the fight. However, maximum aggression level provides little information about the intensity of the fight. Consider the following two scenarios where opponents are engaged in a fight for 10 min: (1) two opponents spend 9 min antennal fencing, 50 s bilateral mandible spread and 10 s grappling with each other; (2) two opponents spend 30 s antennal fencing, 30 s bilateral mandible spread and 9 min grappling with each other. Simply scoring both fights as reaching a maximum aggression score of 6 would ignore the longer durations of highly aggressive behaviour in the second fight. To quantify fight intensity we multiplied each behaviour's aggression score by the total number of seconds it was performed. These weighted aggression scores were then summed across all the behaviours each individual performed. That sum was then divided by the total number of seconds the opponents were engaged in the fight to account for variable fight durations. Neither aggressive songs nor body jerks were included in the quantification of fight intensity.

Statistical analyses

We performed all statistical analyses in JMP v7.0.1 (SAS, Cary, NC, USA). All statistical analyses were based on the behavioural interactions that occurred during a fight, during the post-conflict period, or during the entire contest. We used paired t-tests to ascertain whether winners were more likely than losers to perform aggressive songs or body jerks during fights or after fights. We used backward stepwise regression models with a $p_{\text{leave}} = 0.05$ to quantify the variables that influenced the rate of aggressive song and body jerk production. Predictor variables in these models included: the individual's mass, the contest stage (fight or post-conflict), whether the individual was the winner or the loser, the fight intensity, the fight duration, the interaction between contest stage and whether the individual was the winner or the loser, and the interaction between fight intensity and whether the individual was the winner or the loser. Similarly, we used nominal logistic fit models to quantify which variables influenced whether the individuals performed aggressive song and body jerks or not. We included the same effects as those listed above for the regression models. A Spearman's rank correlation was used to assess whether there was a positive relationship between maximum aggression score and fight intensity.

Because of the multiple statistical comparisons (8 paired t-tests, 2 regression models, 2 nominal logistic fit models and 1 correlation) we used a false discovery rate B-Y adjustment ($\alpha < 0.0157$) to account for the 13 statistical tests that we performed. We opted for the false discovery rate B-Y adjusted alpha instead of the Bonferroni adjustment because the Bonferroni adjustment ($\alpha < 0.0038$ for the 13 statistical tests) has been shown repeatedly to be overly conservative (e.g., Benjamini et al., 2001; Nakagawa, 2004; Narum, 2006).

Results

The majority of fights escalated to the highest level of aggression, grappling (15/19 fights). Of the other four fights, one escalated to the second highest level of aggression, mandible engagement, while the other three escalated to unilateral or bilateral mandible spreading. The average maximum aggression score was 5.52 ± 0.23 on the scale of 0 to 6. Because so many contests reached the most aggressive stage it was difficult to tease apart the differences in aggressiveness between these fights using maximum aggression score. We, therefore, calculated fight intensity as described above. Using this novel fight intensity measure we found that aggressiveness was highly variable across fights, ranging from a score of 1.5 to a score of 5.0 (2.71 ± 0.22), over a 3-fold difference. There was a nearly significant positive correlation between the maximum level of aggression in the fight and the fight's intensity (Spearman's $p_{1,18} = 0.47$, $p = 0.0441$; Figure 1).

Aggressive songs

At least one of the two fighters sang aggressively in all 19 aggressive contests. Winners produced aggressive songs in every contest while losers produced aggressive songs in just over half of the contests (11/19 contests, 58%). Further, winners produced significantly more aggressive songs than losers throughout the contests (winners: 11.79 ± 2.05, losers: 7.42 ± 2.20; paired t-test: $t_{18} = 3.02$, $p = 0.0073$).

During the fight portion of the contests significantly more winners than losers sang aggressively (19/19 versus 11/19; Table 2). Winners and losers did not differ in their aggressive singing rates or in their average durations

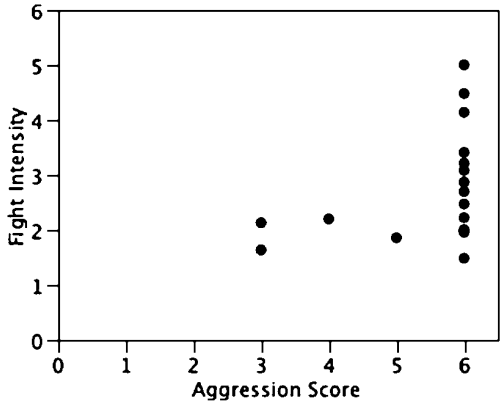

Figure 1. Relationship between maximum aggression score (standard way of scoring the aggression level of a fight) and fight intensity (introduced in this manuscript). This relationship was not quite significant (Spearman's $p_{1,18} = 0.47$, $p = 0.0441$) at the false discovery rate. B-Y adjustment significance level of $\alpha < 0.0157$ required to account for the 13 statistical tests performed in this study.

Table 2. Data on aggressive songs and body jerks for fight winners and losers both during the fight period and the post-conflict period (PC).

Variable	Contest stage	Winner (s, mean ± SE)	Loser (s, mean ± SE)	t/χ^2	p	DF
Mean aggressive song duration	Fight	6.43 ± 1.22	5.13 ± 2.17	0.79	0.4394	18
	PC	5.57 ± 1.33	10.65 ± 9.47	−0.51	0.6136	18
Aggressive song rate (No./min)	Fight	13.13 ± 3.07	6.98 ± 2.58	1.59	0.1292	18
	PC	26.45 ± 5.85	5.99 ± 3.02	4.29	0.0005	18
Proportion of aggressive singers	Fight	19/19	11/19	13.25	0.0015	18
	PC	18/19	7/19	14.15	0.0002	18
Mean body jerk duration	Fight	0.85 ± 0.33	0.12 ± 0.09	2.11	0.0490	18
	PC	1.21 ± 0.26	0.34 ± 0.32	1.90	0.0732	18
Body jerk rate (No./min)	Fight	1.21 ± 0.78	0.02 ± 0.08	1.52	0.1470	18
	PC	2.40 ± 0.72	0.45 ± 0.41	2.23	0.0391	18
Proportion body jerk	Fight	9/19	2/19	6.27	0.0123	18
	PC	12/19	2/19	11.31	0.0008	18

Proportion data were analyzed using Pearson χ^2, all other analyses used paired t-tests. Tests with p values less than $\alpha = 0.0157$ were considered significant.

of aggressive songs. During the post-conflict portion of the contests significantly more winners than losers sang aggressively (18/19 versus 7/19; Table 2). Winners' produced aggressive songs at five times the rate of losers. Win-

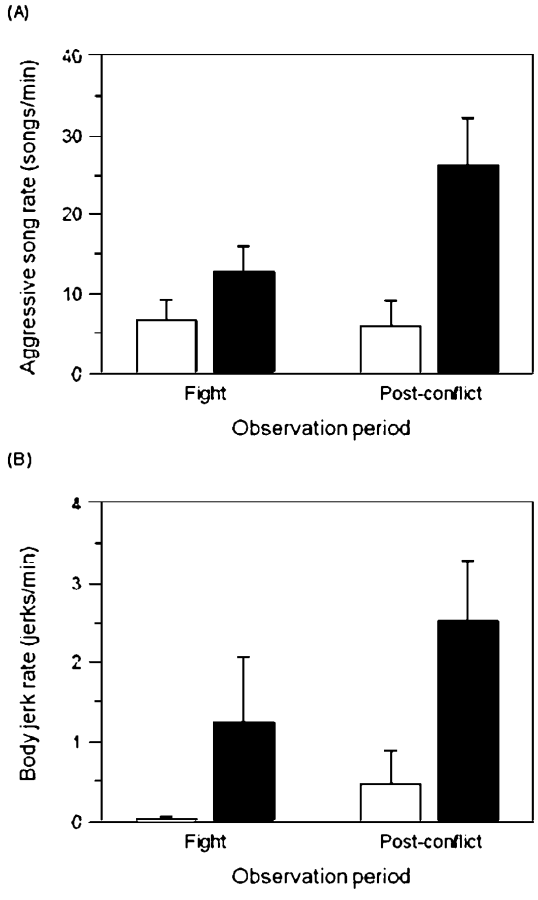

Figure 2. Rate of (A) aggressive song production and (B) body jerk production for winners (dark bars) and losers (light bars) during the fight and post-conflict periods. Heights of the bars represent the mean rates; bar whiskers represent the standard errors. Statistics are presented in Table 2.

ners and losers did not differ in their aggressive song durations. Overall, winners more than doubled their rate of singing between the fight and the post-conflict periods. This rate change resulted in winners singing aggressively at five times the rate of losers during the post-conflict period (Figure 2a).

We used a regression model to investigate the parameters that influenced the rate of aggressive song production. Our model was significant and explained 26% of the variation in aggressive song rate. The three parameters that explained most of the variation were whether the individual was the

Table 3. Backward step-wise regression model results for aggressive song rate and body jerk rate; nominal logistic fit results for whether the individuals sang aggressively or not or whether they produced body jerks or not.

Behaviour	Parameter	t/χ^2	p
Aggressive song rate	Winner/loser	−3.70	0.0004
	Fight intensity	3.37	0.0012
	Duration	−2.22	0.0294
Body jerk rate	Winner/loser	−2.83	0.0060
	Duration	−2.22	0.0297
Aggressive song yes/no	Winner/loser	26.88	<0.0001
	Fight intensity	26.79	<0.0001
	Winner/loser × fight intensity	7.23	0.0072
Body jerk yes/no	Winner/loser	20.35	<0.0001
	Fight intensity	3.60	0.0576

All models were statistically significant and explained 13–72% of the variation in these traits.

Rate of aggressive song regression model: $F = 9.37$, $p < 0.0001$, $R^2_{\text{adj}} = 0.26$.

Rate of body jerk regression model: $F = 6.48$, $p = 0.0026$, $R^2_{\text{adj}} = 0.13$.

Aggressive song or not nominal logistic fit: $\chi^2 = 65.72$, $p < 0.0001$, $R^2_{\text{adj}} = 0.72$.

Body jerk or not nominal logistic fit: $\chi^2 = 22.06$, $p < 0.0001$, $R^2_{\text{adj}} = 0.23$.

winner or the loser of the fight, the fight's intensity and the fight's duration (Table 3). We also used a nominal logistic fit model to investigate the parameters that influenced whether or not an individual sang aggressively. Our nominal logistic fit model was significant and explained 72% of the variation in whether an individual sang aggressively or not. The parameters that explained most of the variation were whether the individual was the winner or loser, the fight's intensity, and an interaction between the fight's intensity and whether the individual was the winner or loser (Table 3).

Body jerks

Body jerks were not observed as often as aggressive songs, only occurring in 79% of the contests (15/19). Winners produced body jerks in 68% (13/19) of the contests while losers only produced them in 16% (3/19). Further, winners produced significantly more body jerks than losers throughout the contests (winners: 2.11 ± 0.50, losers: 0.32 ± 0.22; paired t-test: $t_{18} = 3.92$, $p = 0.0010$).

During the fight portion of the contests significantly more winners than losers produced body jerks (9/19 versus 2/19; Table 2). Winners produced body jerks that were seven times the duration than losers, although this difference that was not statistically significant ($p = 0.0490$) at the significance level of $\alpha < 0.0157$. Winners and losers did not differ in their body jerk rates. During the post-conflict portion of the contests significantly more winners than losers produced body jerks (12/19 versus 2/19; Table 2). Winners' produced body jerks at five times the rate of losers, but this difference was not quite statistically significant ($p = 0.0391$) at the adjusted significance level. Winners and losers did not differ in the average duration of body jerks. Overall, winners doubled their rate of body jerks between the fight and the post-conflict periods. Losers, in contrast, did not significantly alter their rate of body jerks between these two periods. This rate change resulted in winners producing body jerks at five times the rate of losers during the post-conflict period (Figure 2b).

We used a regression model to investigate the parameters that influenced the rate of body jerk production. Our model was significant and explained 13% of the variation in body jerk rate. The parameters that explained this variation in body jerk display rate were whether the individuals won or lost the fight and the fight's duration (Table 3). We also used a nominal logistic fit model to investigate the parameters that influenced whether or not an individual produced body jerks. Our nominal logistic fit model was significant and explained 23% of the variation. The parameters that explained most of the variation were whether the individual won or lost the fight and the fight's intensity.

Discussion

Are aggressive songs and body jerks victory displays?

Both aggressive songs and body jerks occurred during the fight period and the post-conflict period. Further, both winners and losers sang aggressively and performed body jerks. Given this, should these behaviours be called victory displays? We believe they should for the following four reasons. First, winners were much more likely to sing aggressively and produce body jerks after the fight than losers. This finding concurs with that of Logue et al. (2010) for *T. oceanicus*. Second, the winners' aggressive song display

rates and body jerk display rates doubled during the post-conflict period compared to their rates during the fight period. Third, the winners' aggressive song display rates and body jerk display rates were five times the losers' rates during the post-conflict period of the contest. Fourth, our analyses revealed that aggressive song and body jerk performance were dependent on whether the cricket was the winner or loser. Together these results suggest that aggressive songs and body jerks should be thought of victory displays as they are produced most often by the winner and occur most often during the post-conflict period.

We are not the first to call behaviours victory displays when (1) they are performed by both winners and losers and (2) they occur both during conflicts as well as following them. Tropical boubou vocal displays, for example, are sung before, during and after playbacks of aggressive songs. However, boubou vocal displays occur significantly more often after the aggressive playback than before or during the playback (Grafe & Bitz, 2004). While losers never sang after retreating, 11 of the 18 pairs of winners produced the vocal display after the aggressive playback. These findings suggest these vocal displays should be considered victory displays, even though both losers and winners sometimes perform them during the contests (Grafe & Bitz, 2004). Song sparrows also produce vocal displays both during and after their conflicts. Like tropical boubous, song sparrow winners and losers sing during the conflict. While losers do not change their song rate following natural contests, winners show a marked increase following the contests, suggesting that increased song rate is a victory display (Bower, 2005). These studies highlight the quantitative difference between the behaviour of winners and losers following conflicts, and that a majority of agonistic interactions are likely concluded with a post-conflict display.

What are the functions of aggressive song and body jerk victory displays?

Winners may produce aggressive songs and body jerks to indicate to the loser that they are fit and still capable of continuing or escalating the contest (browbeating rationale; Bower, 2005; Mesterton-Gibbons & Sherratt, 2006). Losers may evaluate the signals for complexity, duration, rate, or intensity to determine whether they want to engage the winner in future agonistic contests. If so, aggressive songs and body jerks would function to reinforce dominance and the displays should result in fewer future aggressive acts

compared to when they are not performed. Strong support for this idea was recently found in the oceanic field cricket. Logue et al. (2010) observed agonistic interactions between male *T. oceanicus* that were capable of producing aggressive songs or were incapable of producing aggressive songs (through surgery or a natural mutation). Interactions were more aggressive between males that were incapable of signalling aggressively than they were between males who could signal aggressively. Their findings suggest that aggressive songs do indeed help to mitigate the costs of fighting in *T. oceanicus*. This hypothesis remains untested in *G. veletis* and other field cricket species.

Winners may also produce aggressive songs and body jerks to indicate their success to nearby prospective mates or potential rivals (advertising rationale; Bower, 2005; Mersterton-Gibbons & Sherratt, 2006; Logue et al., 2010). When individuals produce aggressive songs or body jerks, the signal is broadcasted to the surrounding area through acoustic, vibrational, and/or visual cues (Kamper & Dambach, 1985). This suggests that their opponent and other conspecific audience members should be able to detect it (Kamper & Dambach, 1985; Logue et al., 2010). Given cricket densities can be quite high in field crickets (Ritz & Köhler, 2007; Cade, 1981; Alexander, 1961), many agonistic encounters are likely to occur with conspecifics nearby (Alexander, 1961; Rodríguez-Muñoz et al., 2010). It is, therefore, possible that aggressive songs and body jerks may signal success to both the loser and to other conspecifics. Our laboratory is presently testing this idea by determining whether fighters produce more aggressive songs or body jerks in the presence of audiences. Further, we will soon ascertain whether audiences change their subsequent behaviour when experimental crickets are muted prior to fighting compared to un-muted control crickets.

Fight intensity and victory displays

Regardless of the function of conflict displays, Bower (2005) suggested that victory displays should positively correlate with fight intensity since the opponents have invested a large amount of time and energy into the conflict. Our results support this suggestion as fight intensity was one of the model parameters that significantly influenced aggressive song occurrence and rate. This finding corroborates other studies that suggest that the occurrence of post-conflict displays may be dependent on fight intensity. For example, post-conflict displays in black-capped chickadees are more likely to occur

after highly aggressive contests. In contests with pitch-matching (thought to be an aggressive signal), the bird that was pitch-matched by his opponent was more likely to perform a post-conflict display than his opponent (Lippold et al., 2008). Other avian studies, such as the contests involving song sparrows or tropical boubous, also demonstrate that victory displays occur most regularly after the more intense counter-singing exchanges (as reviewed by Lippold et al., 2008).

Comparison of victory displays in field crickets

Gryllus veletis' production of aggressive songs and body jerks are directly comparable to *G. pennsylavicus*, *G. rubens* and *T. oceanicus*. We observed *G. veletis* producing aggressive songs in 100% of the trials and body jerks in 79% of the trials. Similarly, Jang et al. (2008) observed that *G. pennsylvanicus* produced aggressive songs and body jerks in every trial (100%), and *G. rubens* produced them in 81% of the trials. Further, Logue et al. (2010) observed that *T. oceanicus* produced aggressive songs in every trial (body jerks were not quantified). In contrast, Jang et al. (2008) observed that *G. fultoni* and *G. vernalis* only produced aggressive songs occasionally (21 and 34% of the time, respectively) and they did not produce body jerks at all (Jang et al., 2008).

Why are the post-conflict displays of male *G. veletis* more similar to *G. pennsylvanicus, G. rubens* and *T. oceanicus* than to *G. fultoni* and *G. vernalis*? Jang et al. (2008) proposed that burrow, crack, or crevice use could explain the cross-species differences in aggression because crickets that stay in one area are more likely to be territorial and vigorously defend their home (Alexander & Bigelow, 1960). Male *G. rubens* regularly use burrows and male *G. pennsylvanicus* can often be found calling from cracks or crevices (Jang et al., 2008). Male *T. oceanicus* regularly call from refuges in naturally formed hollows, at the base of plants, or within bunches of grass (Bailey & Haythornthwaite, 1998; Evans, 1983). In contrast, male *G. fultoni* and *G. vernalis* do not appear to use burrows, cracks, or crevices (Jang & Gerhardt, 2006). Our findings support this idea as male *G. veletis* also use burrows and cracks (Alexander & Bigelow, 1960).

A word of caution

All of our aggression and post-conflict display data were collected using a small fighting arena (15 × 15 cm) where losers' attempts to flee could result

in him following the edge of the container right back to the winner. This action could then result in the resumption of the fight. While we attempted to control for this by ending the fights when losers exhibited submissive behaviour twice in a row, this is still an issue for any agonistic interactions that are observed in a confined space. Fighting dynamics might be quite different in a large, more naturalistic setting. In nature, once a loser breaks apart from a winner, he could flee, leaving the area entirely and not coming back into contact with the winner again. While our small arena may not be representative of natural conditions, it is 50% larger than most other arenas used to observe and quantify field cricket agonistic encounters (Jang et al., 2008; Judge & Bonanno, 2008).

Conclusions

Both winners and losers frequently performed aggressive songs and body jerks but the winners displayed more often than the losers and the display rates doubled during the post-conflict portion compared to the fight portion of the contest. We conclude that both aggressive songs and body jerks should be considered to be victory displays. Future studies should concentrate on the function of victory displays in crickets, preferably within the framework of a social communication network. To date, most studies have only focussed on the two individuals involved in the contest; they have not taken into consideration how post-conflict displays may affect other observers in the group (Bower, 2005). Investigating eavesdropping and audience effects may allow us to ascertain the function of aggressive songs and body jerks.

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