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Does signalling mitigate the cost of agonistic interactions? A test in a cricket that has lost its song

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Prevailing models of animal communication assume that signalling during aggressive conflict mitigates the costs of fighting. We tested this assumption by staging dyadic encounters between male field crickets, *Teleogryllus oceanicus*, under three conditions: (i) both males could sing aggressive songs, (ii) neither male could sing, and (iii) one male could sing but the other could not. We conducted experiments on males from a Hawaiian population from Kauai that has recently evolved signal loss, and males from a Hawaiian population from the Big Island that has not. Among both populations, interactions between two silent males were characterized by higher levels of aggression than interactions involving one or two singing males. Because the level of aggression is strongly related to the cost of fighting, these data demonstrate that signalling mitigates the cost of fighting. In mixed trials, we found no statistically significant differences between the behaviour of calling and non-calling males in either population. We conclude that there is no evidence that the Kauai population exhibits special adaptations to alleviate the costs of signal loss. Finally, we found that males were much more likely to signal after their opponent's retreat than after their own retreat. Aggressive song therefore meets the definition of a 'victory display'.

Keywords: acoustic signals; animal communication; aggression; coordination games; flatwing mutation; signalling

1. INTRODUCTION

Conflict between individuals arises when critical resources, such as food, territory or sex partners, are limited. Two individuals attempting to secure an indivisible resource may ultimately fight one another to resolve their conflict. Fighting, however, is costly because it requires energy and can result in injury or death. Prevailing models of animal conflicts therefore assume that opponents share a common interest in resolving their conflict without paying the costs of fighting (Maynard Smith & Harper 2003).

Collectively, such models—which include hawk–dove games, war-of-attrition games, and the sequential assessment game—are known as 'coordination games' (Maynard Smith & Harper 2003). These games can be resolved when some asymmetry is revealed, and the inferior competitor backs down. Coordination games that include an option to signal (e.g. Maynard Smith & Price 1973) assume that signals can reveal asymmetries between contestants, and thus help resolve conflicts at an earlier stage of escalation than would be possible if contestants did not signal. There exists, however, remarkably little direct evidence that signalling reduces the

overall costs of animal conflicts (but see Rillich *et al.* 2007). We test this assumption by ablating an aggressive signal in a subset of test subjects, staging contests and observing the effects of signal loss on contest intensity. Contest intensity is a useful proxy for the cost of fighting because intensity is expected to covary strongly with energy expenditure (e.g. Hack 1997) and the risk of injury.

The functional significance of agonistic signal loss is particularly relevant to our study organism, the field cricket *Teleogryllus oceanicus*, because a population of this species has recently evolved an inability to signal. Typical male *T. oceanicus* stridulate their reticulated wings to produce a variety of signals, including calling songs, which attract females, and aggressive songs, which are used during interactions with other males. A genetic mutation rendering some males' wings flat, and thus silent, has recently spread throughout a population of *T. oceanicus* on the island of Kauai (Zuk *et al.* 2006). Selection pressure from the acoustically orienting parasitoid fly, *Ormia ochracea*, appears to have driven the rapid spread of the so-called 'flatwing' phenotype on Kauai (Cade 1975; Zuk *et al.* 2006). Although it is believed that the loud calling song is the primary target of selection, flatwing males are incapable of producing any stridulatory sounds, including aggressive songs (Zuk *et al.* 2006). Flatwings do, however, make the wing motions associated with stridulation (Bailey *et al.* 2008).

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Flatwing males compensate for their inability to attract females with calling song by acting as ‘satellites’ near the few remaining calling males (Zuk *et al.* 2006; Tinghitella *et al.* 2009). Flatwing satellites appear to intercept females attracted by singing males. Satellite behaviour places flatwings in close proximity to both other flatwing males and singing males, increasing the potential for aggressive male–male encounters.

Ablating an animal’s ability to signal (e.g. by surgical muting) can provide insights into signal function (McDonald 1989). Although aggressive song has received less study than other acoustic signals in crickets (Brown *et al.* 2006), several aspects of its functional significance are known. First, it has been established that aggressive song is associated with dominance. Dominant males stridulate more frequently than subordinates during an aggressive encounter, and dominant males, but not subordinates, stridulate after a contest (Alexander 1967; Adamo & Hoy 1995). Second, aggressive song can stimulate aggression under certain conditions. Specifically, males who have just won a fight, are behaving territorially or have just copulated can be induced to fight by lashing them with bristles simulating cricket antennae, but they fight more quickly when aggressive songs accompany the tactile stimulus (Alexander 1967). Finally, males tend to sing aggressive songs after (rather than before) bouts of fighting (Alexander 1967). In *Gryllus bimaculatus* the timing of aggressive song depends on the male’s social rearing condition: males raised in groups sing both during and after contests, whereas isolated males sing only after contests (Adamo & Hoy 1995). Importantly, males often engage in multiple bouts of fighting, so signals delivered after one bout of fighting may precede (or even prevent) subsequent bouts.

In the present study, we staged pairwise interactions with male *T. oceanicus*. Interactions involved two calling males, a calling male and a silent male, or two silent males. Each type of contest was conducted on males derived from a population from the Big Island of Hawaii, in which males were silenced through surgery, and a population derived from Kauai, in which the silent males were flatwings. Our goals were to test the assumption that signalling during agonistic contests mitigates the costs of fighting, to determine whether Kauai males exhibit special adaptations that reduce the costs of silence during male–male interactions and to gain insight into the normal functioning of aggressive songs in male crickets.

2. MATERIAL AND METHODS

We used two laboratory populations of *T. oceanicus* in this study. The ‘Big Island’ population is derived from approximately 12 gravid female crickets collected on the Big Island of Hawaii in 2003. The ‘Kauai’ population was founded by approximately 12 gravid females collected in 2003 from the island of Kauai and supplemented yearly with eggs from 12–20 field-caught gravid females. Female *T. oceanicus* mate multiply, so broods from field-caught females are likely to contain substantial genetic diversity (García-González & Simmons 2005).

Animals were housed in plastic 84 l garbage bins. Juveniles were housed separately from breeders. Embedded in the lid of each bin was a single 60 W incandescent light that provided lighting and heat on a 12 h–12 h reversed

Table 1. Description of the trial types used in this experiment.

trial type	population	male 1	male 2	<i>n</i>
A	Big Island	sham-operated	sham-operated	20
B	Big Island	sham-operated	muted	39
C	Big Island	muted	muted	19
D	Kauai	normal wing	normal wing	20
E	Kauai	normal wing	flatwing	37
F	Kauai	flatwing	flatwing	18

light cycle. Bins contained egg crates for substrate and shade, and a moist cotton pad for oviposition (in adult bins) and moisture. Animals had ad libitum access to food (Purina cat chow) and water. We removed crickets from juvenile bins when they reached the final instar (indicated by fully developed wings). Females were placed in breeding bins and males were isolated in plastic cups with food, water and a section of egg crate.

Two days after isolation, males were weighed and assigned to dyads. Each dyad consisted of males of similar weights from the same population. We discuss size matching further in §3 (see also electronic supplementary material). There were three dyad types and two populations for a total of six trial types (table 1). Dyads were randomly assigned to dyad type, until we met our sample size goals for a given trial type ($n = 20$ for trial types A, C, D and F; $n = 40$ for trial types B and E; we did not achieve all of our sample size goals—see table 1 for actual sample sizes), after which they were randomly assigned to one of the remaining dyad types.

Big Island males were then muted or subjected to a sham operation. A coin flip determined which member of a B trial dyad would be muted. We sedated males by placing them in a freezer (-25°C) for 205 s. We then muted males by removing the plectrum of the wing with surgical scissors. Other males received sham operations that were identical to muting operations except that the wings were not cut. Dyad partners were marked with either one or two dots (randomly assigned) of correction fluid on the pronotum. After surgery, males were returned to their individual plastic cups.

Eight days after their final moult, crickets were placed in plastic arenas ($26 \times 12 \times 15$ cm) to habituate and become territorial. Arenas were divided into half along the long axis with removable cardboard barriers. Size-matched pairs shared an arena, with one male on each side of the barrier. The barrier prevented any physical contact between the males. Each side of the arena contained food, water and a piece of egg crate.

Ten days after their final moult, the arena was moved to a dark testing room, and the food, water and egg crate were removed from the arena. After a 5 min acclimation period, the barrier was removed from the arena, allowing the males to interact. Males were observed until they made contact. After first contact, males were allowed to interact for 20 min. We used a fixed interaction time rather than stopping interactions after one male ‘won’ a fight, but our containers were large enough that males in retreat were able to avoid additional fighting. Interactions were recorded with a digital camcorder (Sony Handicam DVD103; Sony Electronics Inc., San Diego, CA, USA) pointing down on the enclosure. The camcorder was set to ‘night-vision mode’ so that it emitted near infrared (NIR) light and recorded the reflected light in the NIR spectrum. After their trials, males were euthanized by freezing.

One of us (I.O.A.) observed the videos and scored the following behaviours: *stridulation*, *aggression*, *initiation*, *retreat* and *chase*. Stridulation was scored when a male raised his wings, rubbed them together and then lowered them. Normal, sham-operated, flatwing and surgically muted males all exhibited stridulation, although only normal and sham-operated males produced sound while stridulating. Aggression was scored when an animal exhibited any of the following behaviours: biting, wrestling, throwing, kicking, mandible jousting or head butting (Dixon & Cade 1986). Initiation was scored when a male approached and contacted his opponent. Retreat was scored when a male moved away from an opponent after the opponent exhibited initiation or aggression. Chase was scored when a male followed a retreating opponent.

Based on the hypothesis that signalling during agonistic contests mitigates the costs of fighting, we predicted that trials with silent males would be characterized by higher levels of aggression than trials in which males were able to signal. We tested this prediction with a general linear model (GLM) in which *dyad type* (two calling males, one calling male and one silent male, or two silent males) and *population* were fixed factors and the sum of all aggressive acts in the trial (*summed aggression*) was the dependent variable. The variable summed aggression was log transformed to meet the assumption of normality.

We wanted to determine whether silent males were at a competitive disadvantage when interacting with calling males. We did this by comparing the measured behaviours (stridulation, aggression, etc.) of calling males with those of silent males with paired *t*-tests. These comparisons were run separately for trial types B and E.

Next, we asked whether Kauai males exhibit special attributes that might reduce the costs of silence during interactions with calling males. We subtracted the silent male's score from the calling male's score for each behaviour in each trial. The distributions of difference scores were then compared between trial types B and E with *t*-tests. Based on the hypothesis that Kauai males are adapted to mitigate the costs of silence during contests with calling males, we predicted that the difference scores would be lower in the E trials than in B trials. Weight differences between paired males could affect contest outcomes, so we repeated the above tests used only pairs with less than 15 per cent difference in mass and then using size as a covariate.

Finally, we used our data to learn more about the function of aggressive song in calling males. Specifically, we asked whether the number of aggressive songs differed between contest winners (males whose opponents had retreated within the prior 20 s) and contest losers (males who had retreated within the prior 20 s). These data could not be transformed to meet the assumptions of parametric tests, so we analysed them with a Monte Carlo analysis with 10 000 iterations (Manly 2006). Our test statistic was the average number of aggressive songs 20 s after the focal male's opponent retreated minus the average number of aggressive songs 20 s after the focal male retreated.

Monte Carlo tests were run in Microsoft EXCEL (2007, Microsoft Corporation, Redmond, WA, USA) with the POPTOOLS v. 2.7.5 plug-in (Hood 2006). All other analyses were conducted with SPSS v. 15.0 (SPSS 2006). We were attentive to the assumptions of the tests, and transformed data sets when necessary. All tests are two-tailed, with $\alpha = 0.05$. Data are summarized as mean \pm s.e.

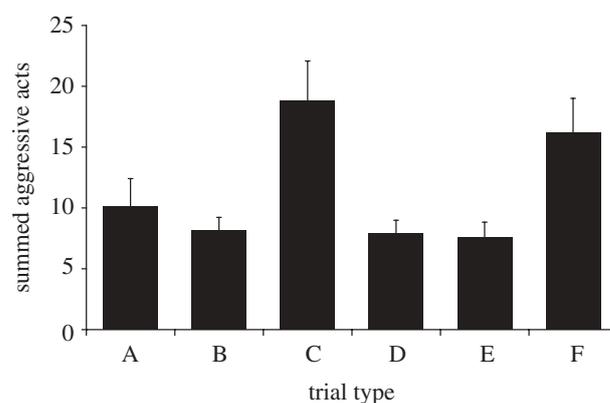


Figure 1. The number of aggressive acts performed by pairs of male *T. oceanicus* as a function of trial type. Trials involved the interaction of two signalling males (A and D), one signalling male and one silent male (B and E) or two silent males (C and F). In a given trial, both subjects were descendants of free-living populations on the Big Island of Hawaii (A–C) or Kauai (D–F). Error bars represent the standard error of the mean. See the text and table 1 for statistics and sample sizes.

3. RESULTS

The GLM testing for the effects of dyad type and population on summed aggression was statistically significant ($F_{5,147} = 4.5$, $p = 0.001$; figure 1). That test revealed a significant effect of trial dyad type ($F_{2,147} = 11.01$, $p < 0.001$), but no significant effects of population ($F_{1,147} = 0.39$, $p = 0.53$) or the interaction dyad type \times population ($F_{2,147} = 0.04$, $p = 0.96$). We used the Ryan–Einot–Gabriel–Welsch *post hoc* test to define statistically heterogeneous subsets among the three dyad types within each population (figure 1). In both populations, we found no difference in aggression between trials with two calling males and mixed trials, but both of these trial types included significantly less aggression than trials with two silent males (Big Island: A = 10.1 ± 2.3 , B = 8.1 ± 1.1 , C = 18.8 ± 3.2 ; Kauai: D = 8.0 ± 1.0 , E = 7.6 ± 1.2 , F = 16.2 ± 2.8).

Paired *t*-tests revealed no significant differences between the behaviour of the calling males and the silent males in either the B or E trials (table 2). Furthermore, the pattern of differences between the behaviour of calling and silent males was indistinguishable between Kauai and Big Island populations (table 3).

The average difference in mass between paired males was 10.0 ± 1.1 per cent. To address the potentially confounding effects of size differences between paired males, we re-ran all relevant analyses excluding dyads with greater than 15 per cent mass difference and (separately) using weight differences as a covariate. The results of these analyses are available as electronic supplementary material. They do not affect our conclusions.

Males sang many more aggressive songs in the 20 s following their opponent's retreat than in the 20 s following their own retreat (Monte Carlo tests; trial type A: after self retreat = 0.36 songs, after opponent's retreat = 9.24 songs, $p < 0.0001$; trial type D: after self retreat = 0.48 songs, after opponent's retreat = 8.28 songs, $p < 0.0001$).

4. DISCUSSION

We set out to address three questions. First, does signalling during agonistic contests mitigate the costs of

Table 2. The results of paired *t*-tests for differences in behaviour between signalling and silent males. A positive mean difference indicates that, on average, signalling males exhibited more of the behaviour than silent males.

group	behaviour	mean difference ^a	s.e.	<i>t</i>	d.f.	<i>p</i>
B	stridulation	5.54 (49.7)	3.11	1.78	38	0.08
B	aggression	1.36 (28.6)	0.86	1.58	38	0.12
B	initiation	0.21 (5.8)	0.77	0.27	38	0.79
B	retreat	-0.74 (-38.7)	0.89	-0.83	38	0.41
B	chase	1.21 (69.1)	0.64	1.89	38	0.07
E	stridulation	-1.73 (-17.1)	4.52	-0.38	36	0.70
E	aggression	-0.16 (-4.3)	0.93	-0.18	36	0.86
E	initiation	-0.14 (-4.1)	0.75	-0.18	36	0.86
E	retreat	0.03 (0.9)	1.15	0.024	36	0.98
E	chase	0.16 (27.3)	0.28	0.58	36	0.56

^aPercentage difference in parentheses.

Table 3. The results of independent-samples *t*-tests comparing behavioural differences between interacting signalling males and silent males from a Big Island of Hawaii population versus a Kauai population. A positive mean difference indicates that the average difference between signalling and silent males is greater in the Big Island population.

behaviour	mean difference ^a	s.e.	<i>t</i>	d.f.	<i>p</i>
stridulation	7.27 (131.2)	5.44	1.34	74	0.19
aggression	1.52 (111.93)	1.26	1.21	74	0.23
initiation	0.34 (165.9)	1.08	0.32	74	0.75
retreat	-0.77 (103.6)	1.44	-0.53	74	0.60
chase	1.04 (86.5)	0.71	1.47	74	0.15

^aPercentage difference in parentheses.

fighting, as assumed by leading models of animal conflict? Fighting is very costly to males in terms of both energy (Hack 1997) and the potential for injury. By comparison, stridulating is an energetically inexpensive behaviour (Hack 1997). We found that interactions between males that could not signal (trial types C and F) were characterized by much more fighting than interactions between signalling males (trial types A and D, respectively). We therefore conclude that signalling substantially mitigates the costs of fighting. This finding supports a critical assumption of coordination games such as hawk-dove games, war-of-attrition models and the sequential assessment game (reviewed by Bradbury & Vehrencamp 1998; Maynard Smith & Harper 2003) that agonistic signals mitigate the cost of conflicts. We found that the cost-saving properties of signalling were apparent when either one or two opponents were capable of signalling. In trials in which only one male could signal, the silent male did not suffer a significant disadvantage (table 2).

As far as we know, this key assumption has not been the subject of a direct test in the past. This lack of testing may be attributed to the intuitiveness of the hypothesis that signalling mitigates the costs of fighting, and to the common observation that animals rarely attack their opponents at the maximum level without signalling first (Maynard Smith & Price 1973). Nevertheless, there exist viable alternative explanations for the existence of signals during agonistic contests (e.g. that they alert bystanders or are non-adaptive responses to stress) and a large body of theory based on coordination game

models, both of which circumstances indicate the importance of testing this assumption directly.

In two previous studies on crickets, researchers induced heightened aggression in crickets by ablating males' sensory systems. Phillips & Konishi (1973) discovered that deafening subordinate males increased their aggression, allowing them to outfight their previously dominant opponents. Their interpretation of these results focused on the proximate basis of the change in behaviour: 'the acoustic signals of the dominant cricket inhibit the aggressive tendencies of the subordinate one' (Phillips & Konishi 1973, p. 64). Rillich *et al.* (2007) found that fights between experimentally blinded male crickets, *G. bimaculatus*, lasted longer and included higher average levels of aggression than fights between sighted crickets. They concluded that, 'visual cues during normal interactions represent external agonistic signals, which suppress aggressiveness between contestants'.

Our second question was whether males in the Kauai population bear special adaptations that reduce the cost of silence during male-male interactions. Although we have not observed aggressive interactions between flatwing males in the wild, their proximity to one another in nature and their readiness to fight in captivity suggest that such interactions probably occur. We found that dyads from the Big Island population and the Kauai population responded similarly to variation in dyad type (figure 1), suggesting that the Kauai population has not evolved special adaptations to cope with silence during male-male interactions, and that there are not behavioural differences in this domain as a result of pleiotropic effects from the mutation. Similarly, we did not find that the effects of silence during calling male versus silent male interactions differed between the two populations (table 3). We therefore conclude that as of 2006 (the last year our laboratory population was supplemented), Kauai males lacked special adaptations to reduce the costs of silence in male-male interactions.

Perhaps we should not be surprised that we did not detect evidence of special adaptation in the Kauai males since the flatwing adaptation has evolved so recently that any complementary adaptation would have had very little time to take hold in the population (Zuk *et al.* 2006). Interestingly, the mean differences in behaviour between calling males and silent males during mixed trials (trial types B and E) were lower in Kauai males than in Big Island males (tables 2 and 3), as we would

expect if the Kauai males were adapting, but these differences were not statistically significant between populations (table 3). It will be interesting to see whether future generations adapt to silence by changing their behaviour. For example, males may become less territorial or use alternative signalling modalities to reduce the high costs of escalated contests. In the meantime, however, the adaptive benefits of silence with respect to avoiding parasitoid-induced mortality appear to balance the costs of silence in the male–male context. Studies examining calling song in the Kauai population have also failed to find evidence of special adaptations to mitigate the costs of song loss, suggesting that pre-existing behavioural plasticity has facilitated the establishment of the flatwing mutation (Bailey *et al.* 2008; Tinghitella & Zuk 2009; Tinghitella *et al.* 2009).

Aggressive song in crickets is generally given after a bout of fighting by the winner of that bout (Alexander 1967; Adamo & Hoy 1995), indicating that it may act as a ‘victory display’. Bower (2005, p. 114) defines a victory display as ‘a display performed by the winner of a contest but not by the loser’. In agreement with that definition, and with prior work on other species of crickets (species not named, Alexander 1967; *G. bimaculatus*, Adamo & Hoy 1995), we found that winners sang many more aggressive songs in the 20 s after a bout of fighting than did losers (25.6 times more in B trials, 17.3 times more in E trials). We therefore conclude that aggressive song meets Bower’s (2005) definition of a victory display. Importantly, however, winning crickets do not restrict their calling to the end of all fighting activity—they often call after a bout of fighting, which may be followed by further fighting later on. Additionally, crickets raised at a high population density emit aggressive song during bouts of aggression (Adamo & Hoy 1995).

Unanswered questions about the function of aggressive song remain. First, to whom is the signal directed: the opponent or other listeners? Our data indicate that songs influence the opponent’s fighting behaviour, suggesting that selection has acted through the opponent’s response to signalling. Experiments conducted in a social context could be used to determine whether ‘eavesdropping’ conspecifics that are not involved in the fight adjust their behaviour in response to a male’s aggressive song (McGregor 1993). Further, we might ask what information is communicated by the aggressive song, and what forces maintain signal honesty? Absolute or relative resource-holding potential may be communicated directly by an unfakeable relationship between body size and signal structure (e.g. Brown *et al.* 2006). Such a hypothesis, however, leads to the prediction that animals should signal before fighting.

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