



Aggressive contests in house crickets: size, motivation and the information content of aggressive songs

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The function of aggressive signals, including both their information content and the circumstances under which they cause resolution or escalation of conflict, continues to be controversial. We studied the information content of aggressive songs in the house cricket, *Acheta domesticus*, to test their ability to inform opponents about fighting ability and motivation. We show that songs produced by individual males are highly repeatable and contain information about male resource holding potential, the ability of a male to win an aggressive contest. Temporal components of aggressive song were correlated with male body size, and size affected both the intensity and outcome of fights. In contrast, we found no components of song that signal motivation to fight. Although males with restricted access to mates were significantly more aggressive and won fights more often, their songs did not reflect the asymmetry in motivation to fight. We discuss possible reasons for the absence of signals of motivation during animal contests.

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Aggressive contests are often accompanied by dramatic visual and acoustic displays that may aid in resolving conflicts before they escalate and threaten the safety of the individuals involved (reviewed by [Huntingford & Turner 1987](#)). Nevertheless, escalated, prolonged and potentially damaging contests occur, particularly when opponents are evenly matched or when the payoff of winning is especially great ([Enquist & Leimar 1990](#)). The actual function of these signals, including both the exact nature of the information content of aggressive signals and the circumstances under which these signals cause either a resolution or an escalation of a conflict, continues to be a controversy ([Vehrencamp 2000](#); [Hurd 2001](#)).

We studied aggression between male house crickets, *Acheta domesticus*, with the goals of determining the potential information content of aggressive displays and the factors determining the initiation, intensity and eventual outcome of aggressive contests. House crickets are a model system for both studies of animal aggression ([Hack 1997](#); [Savage et al. 2005](#)) and studies of acoustic signalling ([Stout et al. 1983](#); [Stout & McGhee 1988](#); [Gray 1997](#); [Ryder & Siva-Jothy 2000](#)), yet remarkably little work has been done to link these two areas of research. Males in many cricket species, including *A. domesticus*, produce aggressive songs with distinct temporal and frequency structures when they encounter a rival male

([Alexander 1961](#)). These aggressive songs are described by [Alexander \(1962\)](#) as a 'brief, sharp signal' that elicits fighting behaviour, reciprocal aggressive stridulation, or retreat. Aggressive songs differ from other cricket songs in their brevity, often being only a single chirp, although in some instances they may be repeated frequently. These songs are thus a signal of aggressive intent, but beyond their use in the context of aggression, we currently know almost nothing about the information content of aggressive songs in crickets.

Our first goal was to test the effects of size-related resource holding potential (RHP) and particularly resource value on the structure and outcome of aggressive contests. Size, of course, is well established as a factor in aggressive contests in many species, but prior studies of aggression in crickets have rarely differentiated the effects of physical size, per se, from condition (size standardized body mass), as we do here. In contrast to the effects of RHP, less experimental work has been done to examine the effects of motivation to fight based on asymmetries in the perception of resource value, particularly in the context of mate competition. Yet, aggressive motivation related to resource value is a central component of evolutionarily stable strategy (ESS) models of animal contests (see [Riechert 1998](#)).

Our second goal was to test whether aggressive songs contain potentially useful information. Early game theory models suggested that aggressive signals are not evolutionarily stable because of strong selection for deceit ([Caryl 1979](#); [Maynard Smith 1982](#); [Krebs & Dawkins 1984](#)). However, subsequent work has shown that evolutionarily stable

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signals of aggression can come about in two ways. First, signals may reliably and honestly communicate RHP, either through direct costs of signal production or through physical constraints that allow signal parameters to be an index of RHP (i.e. handicaps and index signal, respectively) (Zahavi & Zahavi 1997; Vehrencamp 2000). Second, signals may indicate the level of motivation to fight using parameters that are arbitrary with respect to RHP (i.e. conventional signals). Honesty here is maintained by a high cost of retaliation paid by individuals that bluff strength when they are actually weak (van Rhijn 1980; van Rhijn & Vodegel 1980; Enquist 1985; Johnstone & Norris 1993; Hurd 1997). According to handicap models, at the ESS, senders with greater potential benefits may signal a greater motivation to fight (Godfray 1991; Maynard Smith 1991; Johnstone & Grafen 1992). In addition to RHP and motivation, aggressive signals may also inform rivals about the outcome of prior contests. For example, colour badges in several birds appear to be conventional signals of dominance status associated with prior fighting success (Rohwer 1982; Lemel & Wallin 1993; Qvarnström 1997). Acoustic signals may be particularly able to convey short-term changes in motivation and dominance because they can vary over short periods (Vehrencamp 2000).

We show that size, condition and resource value all contribute to the structure or outcome of male–male aggression over access to mates. Moreover, male aggressive songs contain information about RHP and the songs of individual males change after the experience of winning a contest in ways that may signal male dominance. However, despite strong effects of resource value on levels of aggression and the outcome of fights, we found no evidence that males signal their relative motivation to fight within their aggressive songs, and we discuss why it may be adaptive for animals in many contexts not to signal aggressive motivation.

METHODS

Cricket Culturing

Crickets were purchased as late-instar juveniles from reptilefood.com (Dayton, Ohio, U.S.A.) and reared to adulthood in the laboratory. Upon receipt, we housed crickets in 55-litre plastic pails with approximately 250 crickets per pail. Several cardboard egg cartons were provided as substrate and shelter. We fed crickets an ad libitum diet of dry cat food (Special Kitty, Wal-Mart Stores, Inc., Bentonville, Arkansas, U.S.A.), and lightly sprayed water into the pails every second day. Crickets were held at 21°C on a 12:12 h light:dark cycle set for lights off at noon. House crickets display peak activity within 3 h of dusk; this light cycle focused their peak activity in the early afternoon, which was convenient for data collection.

Experiment 1: Do Songs Indicate Resource Holding Potential?

Our goal was to match the structure of aggressive songs with measures of male RHP, including (1) body size, (2)

condition and (3) prior fighting success. Sixty-four adult males were removed from rearing pails and housed individually in 15 × 9 × 12-cm plastic containers with a piece of egg carton for shelter and ad libitum cat food. All males were held individually for 3 days prior to recording their aggressive songs and staging encounters with rival males. This period of acclimation to a solitary environment was performed to standardize male experience and to reduce the stress of frequent social encounters, which may reduce male aggression (Alexander 1961).

Immediately before recording, we measured body size (length of the left hind tibia) using digital forceps and we measured body mass to 0.01 mg using an A&D HR-202 balance (A&D Engineering, Inc., Milpitas, California, U.S.A.). Each male was then placed into a container that was divided into two 7.5 × 9 × 12-cm chambers by a wire screen. To stimulate aggression over a potential mate, we placed a single female cricket into a screen tube (ca. 1.5 × 3 cm), which was then placed adjacent to the screening within one of the chambers. We placed the experimental male into the same chamber as the female and a rival 'stimulus' male in the opposite chamber. We temporally muted the stimulus male before placing it into the chamber by reversing its forewings so that the plectrum of the right wing could not engage the file of the left wing. Both male crickets could engage in mutual antennal contact and could antennate the female. This contact stimulated the experimental male to produce aggressive song, but did not allow escalated aggression. Stimulus males similarly vibrated their wings after antennal contact, without producing song. We recorded these 'pre-fight' calls using a Sony Professional Walkman WM-D6C (Sony Corp., Tokyo, Japan). To help ensure that we analysed male–male aggressive song, we used only songs that we judged to be directed towards the stimulus male. We recorded a minimum of three discrete sequences of aggressive song for each male. All songs were recorded in a temperature-controlled room maintained at a constant temperature of 21°C to avoid fine-scale temperature effects on song structure (Martin et al. 2000). Temperature within the recording chamber was measured with a Springfield PreciseTemp temperature probe (Springfield Precision Instruments, Wood Ridge, New Jersey, U.S.A.). Muted stimulus males were not used in subsequent aggression trials.

We then staged encounters between two experimental males ($N = 32$) in arenas created from 27 × 16 × 12-cm plastic buckets. We used an arena foreign to both males to avoid any effect of territory ownership on fight outcome. The buckets were thoroughly washed and rinsed with 70% ethanol prior to each encounter to remove any residual pheromones. In the centre of the arena we placed a screen tube containing a female (different from that used to stimulate pre-fight song). Males were then randomly paired and each male was given a distinctive marking with coloured typewriter correction fluid for identification. We placed the two males on opposite sides of the arena and allowed them to interact.

In this environment, male house crickets typically engage in a series of aggressive encounters. We defined the encounters to begin with physical (usually antennal) contact and to end when one male retreated by at least

10 cm. We recorded (1) the number of encounters occurring within 15 min of initial contact, and we ranked the intensity of each aggressive encounter on a scale from 1 to 6 based on the level of escalation by each male, following Alexander (1961). Briefly, a level-1 contest involves a retreat of one male after antennal fencing, a level-2 contest involves mutual antennal fencing, a level-3 contest involves unilateral mandible spreading, a level-4 contest includes bilateral mandible spreading, a level-5 contest involves mandible locking, and a level-6 contest involves mandible locking and wrestling (see Alexander 1961 for full details). In addition, for the first encounter we identified the male that initiated the first physical contact and the male that initiated aggression (defined as the male that performed the first aggressive act), and for each encounter we recorded which male retreated. The male making the majority of retreats within the 10-min span of encounter was judged the loser.

To examine the change in song structure after a fight, we recorded the 'post-fight' aggressive songs of winners immediately after they won. These males were separated from the loser and placed back into the recording arena across a screen from a muted stimulus male. Again, a minimum of three aggressive songs was recorded for each male. Losers typically retreat and become silent and thus we were unable to record post-fight songs from these males.

Analysis of Aggressive Song

We digitized the songs using an Audiophile 2496 Audio Accelerator Card (M-Audio USA, Arcadia, California) and Canary Software (version 1.2; Cornell Laboratory of Ornithology, Ithaca, New York, U.S.A.) on a Macintosh G4 computer. For each of the three song sequences, we digitized sequences of approximately 30 s and then chose a random pulse within a random chirp for analysis. We measured four components of song temporal structure and two components of song frequency (pitch). Figure 1 shows a waveform of aggressive song; aggressive song is characterized by a series of pulses grouped into discrete rhythmic chirps. For song structure, we measured pulses per chirp, pulse duration (ms), pulse interval (ms) and chirp interval (ms) (Fig. 1). For frequency, we measured the peak frequency of the pulse (kHz) and Δ frequency, which is the range of frequencies within the pulse (kHz).

Significant information content of a signal such as aggressive song requires signal consistency. We analysed signal consistency as the repeatability (single-measure intraclass correlation coefficient) of components of aggressive song using within-subjects ANOVA. We analysed repeatability of song structure for a subset of males ($N = 21$) by averaging up to three measures of each component of song structure within a single chirp and comparing these values between two chirps of a given male recorded more than 30 s apart. For five of these males, each of the songs contained only a single chirp and thus $N = 16$ for the repeatability of chirp interval.

Next, we analysed the relation between songs and male phenotype for all 64 males. The large number of variables involved in these analyses produced two problems for the

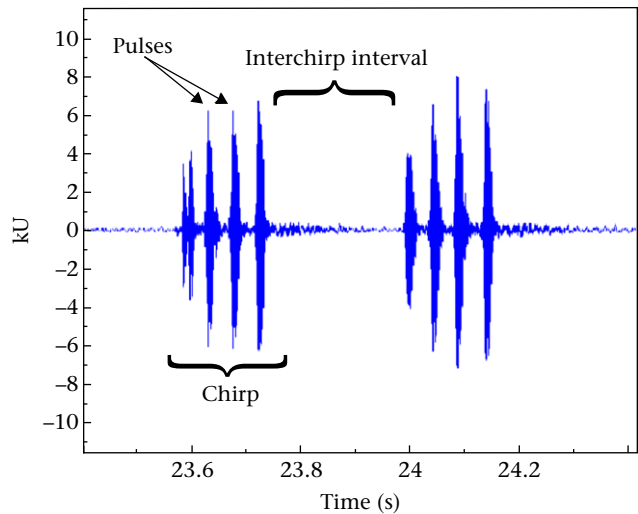


Figure 1. A waveform showing the temporal structure of approximately 1 s of *Acheta domestica* aggressive song. The X-axis scale is time (s) and the Y-axis scale is in 'kilounits', which are proportional to the sound pressure level.

statistical analyses. First, use of multiple testing would substantially increase type I statistical error (falsely rejecting the null hypothesis). Second, several song characters were highly correlated, and separate tests of correlated variables are not statistically independent. In the analyses of pre-fight songs, we dealt with these problems by first reducing the number of song characters using principal components analysis (PCA). We then used multiple regression analysis, with three principal components (PCs) (see Results) entered as independent variables, and physical size (tibia length) and condition entered as the dependent variables in two separate analyses. Condition was measured as the residual of the exponential regression of size on body mass; thus males in better condition were relatively heavy for their tibia length and males in poorer condition were relatively light (Jakob et al. 1996). We followed up cases in which a PC was significantly related to size or condition, with multiple regression analyses using the raw song characters that loaded most heavily on these PCs (loadings $\geq |0.5|$) to identify the song characters most likely to contain information about size and condition. We also compared PCs of winners and losers using paired t tests.

Comparison of pre- and post-fight song precluded variable reduction using PCA because here each male contributed two sets of song character values, which would result in a pseudoreplicated PCA. Therefore, we compared songs of individual males produced before and after winning a fight using paired t tests of all six song characteristics. We were unable to record post-fight song of five winning males, and thus $N = 27$. We report P values before and after sequential Bonferroni adjustment (listed as P_{sB}) for multiple testing.

Experiment 2: Does Perceived Resource Value Affect Songs and the Outcome of Aggression?

Our goal here was to test whether perceived value of a resource would affect male motivation to fight and if

males would signal aggressive motivation in their songs. The resource in question was perceived mating opportunities and we altered resource value by experimentally manipulating male access to females prior to testing. Males, different from those used in experiment 1, were individually housed in plastic buckets with food, an egg-carton shelter, water and a light cycle identical to the conditions in experiment 1. Males received either (1) nightly encounters with a female for four consecutive nights ('paired' treatment) or (2) no female encounters ('solitary' treatment). Each female was collected from the large population cage and added to a male's cage at the beginning of 'lights-off' and removed 12 h later at 'lights-on'. Each female was then returned to the population cage. Thus, males were probably exposed to a different female each night.

Aggressive songs were recorded as in experiment 1 with the exception that no post-fight songs were recorded. We were only interested in the effects of exposure to females, not prior aggression, on song characters. We used discriminant function analysis (DFA) to test the degree to which song characters would classify males into the two treatment groups.

We then tested the effect of perceived resource value on male aggression. We predicted that the males with less exposure to females would perceive mating opportunities to be more valuable and, thus, would be more motivated to fight over potential mates. To test these predictions, we paired males from alternative treatments by body mass to minimize differences in RHP. We then allowed these males to fight in the presence of a screened-off female (as in experiment 1). Again, we staged contests in a neutral arena to avoid territory ownership effects on fight outcome. We recorded who initiated physical contact, who initiated aggression (by performing the first aggressive act), and who won the fight (as above). We also recorded the number and intensity of each bout of fighting, as in the previous experiment.

Effects of treatment on initiating contact, initiating aggression and winning the fight were analysed using logistic regression, with treatment of initiator or winner as the binomial dependent variable and relative size and relative condition as covariates. We calculated relative size and relative condition as: ((value of winner - value of loser)/average of winner and loser).

Paired males have higher female encounter rates, which we predicted would decrease their motivation to fight over a female. However, paired males may also expend more energy courting females or engaging in general social interactions. Thus, a difference between treatments could be due to either perceived resource value or more frequent social interactions, independent of resource value. We address this issue in two ways. First, we measured body mass and condition immediately before song recordings and aggression trials to assess whether male condition differed with treatment; there was no significant treatment effect on either condition ($t_{110} = 0.26$, $P = 0.50$) or body size ($t_{110} = 0.67$, $P = 0.80$). Second, we tested treatment effects in relation to two different resources, mates or food. Differences in perceived resource value should only affect aggression over females, whereas differences related to

general social interactions should affect aggression over any resource. We added a treatment to the experiment in which solitary and paired males were restricted of food for 3 days and then paired in the presence of food resources (a single piece of hard cat food), rather than a female. Aggressive behaviour was recorded as outlined above.

RESULTS

Experiment 1

Fight outcome

Winners of fights were in significantly better condition than losers (0.0120 ± 0.0070 versus -0.0083 ± 0.0068 , respectively; logistic regression: Wald statistic: $W_1 = 5.43$, $P = 0.02$; Fig. 2b). There was no significant difference in the size (tibia length) of winners and losers (7.13 ± 0.09 versus 6.93 ± 0.10 mm, respectively; $W_1 = 2.04$, $P = 0.15$; Fig. 2a). However, smaller males fought harder to win fights; fight intensity was significantly negatively correlated with

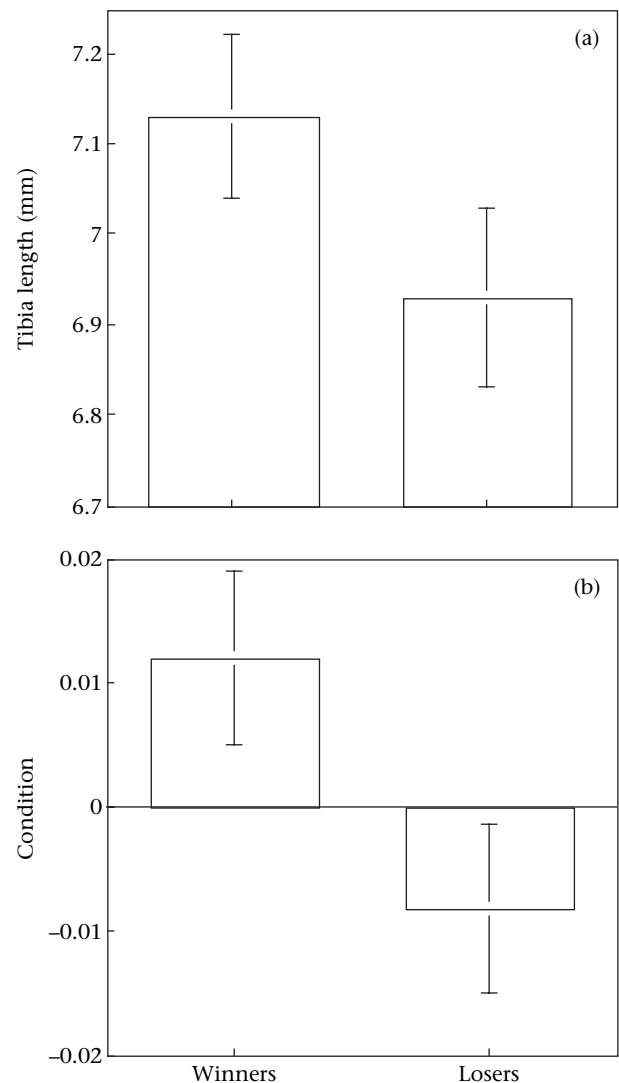


Figure 2. Mean \pm SE (a) tibia length and (b) condition of winner and loser male crickets engaged in contests over females.

relative body size (Pearson correlation: $r_{30} = -0.38$, $P = 0.03$), such that the closer in size of the eventual winner to the loser, the more intense the fight ranking. When winners were much larger, fights were settled at lower intensity. There was no significant correlation between relative condition and fight intensity ($r_{30} = 0.005$, $P = 0.98$).

Analysis of pre-fight songs

Song variables generally had a very high level of repeatability (Table 1). All temporal measures of song structure (pulses per chirp, pulse duration, interpulse interval and chirp interval) were significantly repeatable, as was peak frequency. Δ frequency was not significantly repeatable.

Using PCA, we identified three components that collectively explained 69.9% of total variance in song characters (Table 2). Pulse duration, pulse interval and chirp interval each loaded most heavily on PC1, which we consider to be a measure of song temporal structure. Δ frequency loaded most heavily on PC2. Pulses per chirp and peak frequency loaded most heavily on PC3.

Multiple regression showed a significant overall relationship between the three principal components of song and male body size ($R = 0.44$, $N = 64$, $P = 0.005$). PC1 (temporal structure) significantly decreased ($\beta = -0.25$, $t_{62} = 2.04$, $P = 0.046$) and PC3 (peak frequency and pulses per chirp) significantly increased ($\beta = 0.37$, $t_{62} = 3.18$, $P = 0.002$) with male size. PC2 (Δ frequency) was not significantly associated with male size ($\beta = -0.05$, $t_{62} = -0.45$, $P = 0.65$). The principal components of song were not significantly associated with male condition (multiple regression: $R = 0.20$, $N = 64$, $P = 0.47$).

Of the three song characters that loaded most heavily on PC1, only interpulse interval was significantly related to male size (Pearson correlation: $r_{62} = -0.33$, $P = 0.01$); larger males had shorter interpulse intervals. Neither of the other two song characters was significantly related to male size (pulse duration: $r_{62} = 0.13$, $P = 0.31$; chirp interval: $r_{62} = -0.06$, $P = 0.64$). Of the two song characters that loaded most heavily on PC3, only pulses per chirp was significantly related to male size ($r_{62} = 0.30$, $P = 0.02$; peak frequency: $r_{62} = 0.10$, $P = 0.41$).

Winners had significantly lower PC1 (temporal structure) values than losers (paired t test: $t_{31} = -1.81$, $P = 0.04$), suggesting that males with greater pulse duration, smaller pulse intervals and smaller chirp intervals won more fights. PC2 (Δ frequency) ($t_{31} = 0.80$, $P = 0.22$) and PC3 (pulses per

Table 1. Repeatability of six components of aggressive song

| | r_1 | F | df | P |
|----------------------------|-------|-------|--------|---------|
| Temporal structure | | | | |
| Pulse duration | 0.75 | 4.05 | 20, 20 | 0.0015 |
| Interpulse interval | 0.83 | 5.77 | 20, 20 | 0.0001 |
| Pulses per chirp | 0.57 | 2.34 | 20, 20 | 0.032 |
| Chirp interval | 0.97 | 34.24 | 15, 15 | <0.0001 |
| Frequency structure | | | | |
| Peak frequency | 0.72 | 3.57 | 20, 20 | 0.0032 |
| Δ Frequency | 0.30 | 1.43 | 20, 20 | 0.22 |

r_1 = The infraclass correlation coefficient.

Table 2. Loadings and percentage variance explained by three principal components of the six song characters

| Song character | Component | | |
|---------------------|-----------|-------|-------|
| | 1 | 2 | 3 |
| Pulse duration | -0.84* | 0.22 | -0.16 |
| Interpulse interval | 0.75* | -0.09 | -0.32 |
| Chirp interval | 0.64* | -0.12 | -0.18 |
| Peak frequency | 0.32 | 0.23 | 0.48* |
| Δ Frequency | 0.06 | 0.78* | 0.24 |
| Pulses per chirp | -0.09 | -0.43 | 0.73* |
| % Variance | 34.19 | 18.31 | 17.39 |

*The corresponding song character loaded most heavily on this component.

chirp and peak frequency) ($t_{31} = 0.97$, $P = 0.17$) did not differ significantly between winners and losers.

Comparison of pre- and post-fight songs

Males significantly increased Δ frequency after winning a fight (paired t test: $t_{26} = -3.40$, $P = 0.002$, $P_{SB} = 0.02$). No other song characters were significantly changed (pulses per chirp: $t_{26} = -0.48$, $P = 0.64$; pulse duration: $t_{26} = 0.04$, $P = 0.97$; interpulse interval: $t_{26} = 2.12$, $P = 0.04$, $P_{sb} = 0.22$; chirp interval: $t_{26} = 1.55$, $P = 0.07$; peak frequency: $t_{26} = 0.64$, $P = 0.53$).

Experiment 2

Effects of treatment on aggression

Restricting access to females significantly increased the rate at which males initiated aggression and affected the outcome of fights. There was no effect of treatment on the frequency of initiating physical contact (Table 3). However, once in contact, solitary males initiated 80% (45 of 56) of the aggressive encounters and won 67% (34 of 51) of the fights. Relative size and relative condition did not significantly affect initiation of physical contact or initiation of

Table 3. Logistic regression of treatment (solitary versus paired male), relative size and relative condition on the frequency of initiating contact, initiating aggression and winning the contest

| | Ratio | Wald statistic | df | P |
|------------------------------|-------|----------------|----|--------|
| Initiating contact | | | | |
| Treatment (solitary:paired) | 32:24 | 1.11 | 1 | 0.29 |
| Relative size | — | 0.03 | 1 | 0.87 |
| Relative condition | — | 0.01 | 1 | 0.92 |
| Initiating aggression | | | | |
| Treatment (solitary:paired) | 45:11 | 13.61 | 1 | <0.001 |
| Relative size | — | 3.61 | 1 | 0.08 |
| Relative condition | — | 0.03 | 1 | 0.86 |
| Winning contests* | | | | |
| Treatment (solitary:paired) | 34:17 | 6.38 | 1 | 0.012 |
| Relative size | — | 4.91 | 1 | 0.027 |
| Relative condition | — | 7.39 | 1 | 0.007 |

*In five encounters neither male won a clear majority of aggressive contests; these were judged to be 'ties' and were excluded from analysis of winning contests.

aggression (Table 3), but despite being paired by body mass, larger males and males in better condition won more fights (Table 3).

If this difference in aggression was due to perceived resource value, the following two predictions should hold. First, treatment effects should be resource dependent: solitary males should only be more aggressive than paired males when they are fighting over potential mates. Second, solitary males should be more willing to escalate fights over females. That is, if solitary males perceive greater benefits, they should be willing to incur greater costs and fight with greater vigour before giving up a fight. In contrast, if paired males perceive mates as being readily available, they may concede the fight at a low intensity of aggression. Thus, we predicted that fights lost by solitary males would have greater intensity rank than fights won by solitary males.

Supporting the first prediction, type of resource (food or mates) had a significant effect on who initiated aggression; solitary males were significantly more likely to initiate aggression over females than over food (Table 4), but showed similar overall fight intensities when competing for food ($\bar{X} \pm \text{SE}$: 2.5 ± 0.17) and mates (3.1 ± 0.22). Within the food aggression trials, there was no significant effect of treatment on initiation of aggression (Table 4).

We tested the effect of treatment on willingness to escalate using two measures of intensity of aggression: number of bouts of fighting and average intensity ranking. Multivariate ANOVA, incorporating both variables, revealed a significant overall effect of treatment on aggressive intensity (Wilk's $\lambda = 0.88$, $F_{2,53} = 3.79$, $P = 0.029$; Table 5). In both cases, fights lost by solitary males had values indicating greater intensity of aggression; univariate comparisons showed a statistically significant difference for number of bouts and a marginally nonsignificant difference for average intensity ranking.

Comparison of the aggressive songs of solitary and paired males

DFA correctly classified only 51% (26 of 51) males into their treatment groups (Wilk's $\lambda_6 = 0.96$, $P = 0.92$), and no single song character differed significantly between groups (pulses per chirp: $F_{1,49} = 0.22$, $P = 0.64$; pulse duration: $F_{1,49} = 0.03$, $P = 0.87$; interpulse interval: $F_{1,49} = 0.91$, $P = 0.35$; chirp interval: $F_{1,49} = 0.13$, $P = 0.72$; peak frequency: $F_{1,49} = 0.14$, $P = 0.71$); Δ frequency: $F_{1,49} = 0.41$, $P = 0.53$).

Table 4. The effect of resource on initiating aggression and average fight intensity

| | Resource | |
|---|-----------------|-----------------|
| | Females | Food |
| Initiating aggression* | | |
| Solitary | 45 | 13 |
| Paired | 11 | 10 |
| Fight intensity ($\bar{X} \pm \text{SE}$) | 3.07 ± 0.22 | 2.51 ± 0.17 |

* $\chi^2_1 = 4.75$, $P < 0.05$.

Table 5. Comparisons of the intensity and number of bouts for contests won by solitary versus paired males

| | Winner | | F | df | P |
|-------------------------|----------------|----------------|------|------|------|
| | Solitary | Paired | | | |
| Mean \pm SE intensity | 1.9 ± 0.10 | 2.3 ± 0.23 | 2.98 | 1,54 | 0.09 |
| Number of bouts | 6.0 ± 0.38 | 7.8 ± 0.87 | 5.04 | 1,54 | 0.02 |

DISCUSSION

Size and Condition are Components of RHP

Male crickets engage in aggressive and occasionally escalated contests over females (Otte & Cade 1976; Tachon et al. 1999), with winners typically achieving greater mating success (Cade 1979; Burk 1983; Nelson & Nolen 1997; Savage et al. 2005). Hack (1997) showed that, in male house crickets, winners of aggressive encounters are generally heavier than their opponents and the winner's total energetic expenditure usually exceeds that of the loser.

Our results reinforce the view that body mass is the most important determinant of RHP in crickets and most other animals (Alexander 1961; Dixon & Cade 1986; Simmons 1986; Souroukis & Cade 1993; Hack 1997; Nosil 2002; Shackleton et al. 2005; but see Tachon et al. 1999). However, rather than looking solely at body mass, we partitioned overall mass into components representing (1) linear skeletal size (tibia length) and (2) deviation of wet mass from the relationship predicted by skeletal size, which we call condition (Jakob et al. 1996). Both tibia length and condition influenced the outcome of aggression. In both experiments, males in better condition (heavy for their size) won significantly more fights. Tibia lengths of winners were significantly greater than those of losers in experiment 2 but not in experiment 1. However, in experiment 1, smaller males had to fight harder than larger males to win their fights. Thus, size and condition are key components of male resource holding potential, and it would be mutually advantageous for rivals to communicate size and condition during aggressive contests. Nevertheless, it is also clear that size and condition are not the only factors determining the outcome of aggression; 37.5% of males in experiment 1 (12 of 32) won fights despite having lower body mass, and 12.5% (4 of 32) of these males had both smaller size and poorer condition. In a study of *Gryllus bimaculatus*, heavier animals lost 30% of fights (Hofmann & Schildberger 2001). High motivation to fight may help animals to overcome inferior fighting ability (e.g. Wagner 1989; Neat et al. 1998; Kotiaho et al. 1999).

Aggressive Songs Indicate Resource Holding Potential

Song structure carries significant information about male identity and aspects of male phenotype that relate to RHP. Aggressive songs differ between males and show high short-term repeatability in temporal structure and peak frequency. Such consistency of song structure is a requirement

for the communication of resource holding potential. Body size was significantly correlated with the principal component that encompassed most of the variation in three major temporal components of songs (pulse duration, pulse interval and chirp interval), although, of these characters, only pulse interval was significantly correlated in univariate analysis. Larger males had shorter pulse intervals and thus produced pulses more rapidly within chirps. Body size was also positively correlated with the number of pulses per chirp. We point out that, although our results show a correlation between song and RHP, we did not test whether males use this information to affect contest outcome. This is a goal of future studies.

Although no previous studies have analysed the relationship between male size and aggressive song in crickets, there appears to be information about size in other forms of cricket song. For *A. domesticus*, Gray (1997) reported that males with greater body mass broadcast calling songs that are both louder and have more pulses per chirp. This matches our finding that pulses per chirp within aggressive song increases with male body size. Females, in turn, preferred the calling song of larger males, apparently because of differences in pulses per chirp (Gray 1997). Studies of other crickets and katydids indicate size-related variation in various aspects of calling or courtship song, including peak frequency (Latimer & Sippel 1987; Bailey & Yeoh 1988; Gwynne & Bailey 1988; Simmons & Zuk 1992; Brown et al. 1996; Mason 1996) and some temporal components (Simmons & Zuk 1992; Tuckerman et al. 1993; Brown et al. 1996). We note, however, that the r^2 values for the correlations between song characters and size were generally fairly low (0.11 or lower in this study). Thus, assessment of body size from song, if it occurs, may often be inaccurate. Other studies have also reported no relationship between calling song structure and size in crickets, or inconsistent relationships (see Gerhardt & Huber 2002).

Previous studies have often failed to find any condition-dependent components of cricket song. Gray & Eckhardt (2001) showed that neither diet, male residual mass, nor fat reserves was correlated with temporal or frequency-related song characters in the courtship song of the field cricket, *Gryllus texensis*. This is consistent with our results of a lack of condition-dependent temporal and frequency structure in the aggressive songs of house crickets. In *Gryllus lineaticeps*, there is no relationship between the diet and chirp rate in the courtship song (Wagner & Reiser 2000), but chirp rate increases with diet quality in calling song (Wagner & Hoback 1999). In *Gryllus campestris*, chirp rate increases with current condition (Scheuber et al. 2003a) and carrier frequency increases with prior condition during nymphal development (Scheuber et al. 2003b). Ryder & Siva-Jothy (2000) reported that immune function, which may be related to condition, was positively correlated with pulses per chirp in *A. domesticus*.

Do Aggressive Songs Indicate Prior Fighting Success?

Information about prior fighting success is often difficult to distinguish from RHP, because dominance and RHP

are naturally correlated. For example, Crankshaw (1979) reported that dominant male *A. domesticus* had lower chirp rates and a 'brighter' chirp, and females showed a phonotactic preference for the calling songs of dominant males. We do not know, however, whether females preferred cues of dominance (i.e. prior winning), per se, or cues of dominance-related RHP. Nevertheless, the experience of winning a contest may determine the outcome of contests irrespective of RHP in species such as the speckled wood butterfly, *Pararge aegeria* (Davies 1978) and copperhead snakes, *Agkistrodon contortrix* (Schuett 1997). The importance of prior fighting success in cricket aggression was demonstrated by Adamo & Hoy (1995), who found that male *Gryllus bimaculatus* that lost fights ceased displaying aggressive behaviour for 10 min, whereas winners attacked other males more quickly. For male *A. domesticus*, neither peak frequency, nor any temporal component of aggressive song significantly changed after winning a fight. Males, however, called considerably more vigorously after the retreat of a rival, and defeated rivals almost never called. Thus, the simple presence of song contains information about prior success in an aggressive contest. Males also altered Δ frequency after winning a fight. A likely explanation for more vigorous singing is that fight outcome provides males with an external measure of their RHP, and that when winners perceive a lower cost of engaging in future contests, they are more willing to advertise aggressive intent to new rivals over a greater distance. Interestingly, aggressiveness of subordinate crickets is restored following brief periods of flight (Hofmann & Stevenson 2000; Savage et al. 2005).

Perceived Resource Value Affects the Initiation, Intensity and Outcome of Aggression

Males significantly altered aggression according to perceived resource value. In the presence of a potential mate, males isolated from females for 4 days were significantly more likely to initiate aggression, compared to males that encountered females during the previous 4 nights. This difference in aggressive motivation occurred only in the presence of a female, and not in the presence of food resources, which would have been equally valuable to both males. Overall fight intensity was similar between fights over females and fights over food, but solitary males were more frequently the aggressors only during fights over females. Thus, males appeared to be showing a selective response to different valuations of the resource (mating opportunities) rather than a generalized difference in aggression under all conditions.

In our experiment on perceived resource value, size and condition had no significant effect on initiating aggression, but both of these components of resource holding potential affected the likelihood of winning a fight. Thus, for inexperienced males, perceived resource value appears to dominate initial motivation to fight, but resource holding potential becomes increasingly important for determining the outcome once the fight has begun. Nevertheless, solitary males won significantly more fights

than did paired males, showing that motivation caused by greater perceived resource value can override at least small differences in resource holding potential. Moreover, solitary males engaged in significantly more escalated contests before losing fights, suggesting that solitary males invest more energy in aggression before conceding defeat.

Motivational asymmetries also affect the outcome of fights over food in *A. domesticus*. Nosil (2002) showed that size predicts the winner of fights over a food pellet when both contestants are equally hungry but motivation becomes the predominant factor when hunger levels differ.

Males Do Not Advertise Resource Value

In another study of motivation asymmetry during aggression over mates, Poole (1989) showed that male African elephants, *Loxodonta africana*, in musth signal motivational state, and smaller but more motivated males often win contests. In our case, despite these clear differences in male motivation to fight for mates, there was no significant difference in the aggressive songs of solitary and paired males. Thus, males do not appear to advertise perceived resource value in the structure of their songs. So the question becomes, why advertise RHP but not level of motivation, particularly when both affect the outcome of a contest? One very likely possibility is that, unlike RHP, advertising motivation is often equivalent to advertising resource value, the payoff of winning. Males relatively uninformed about resource value might thus receive valuable information from opponents that alter their signals according to the payoff, possibly attracting more prolonged and costly aggression. Clearly this is disadvantageous for the male providing the signal. Thus, although motivation is expected to have a strong influence on the structure of aggressive contests, males are not expected to communicate aggressive motivation to the extent that it signals general resource value. In cases such as African elephants, motivation may be signalled because it is not correlated with general resource value, per se (Poole 1989).

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