



Assessment of strength and willingness to fight during aggressive encounters in crickets*

HANS A. HOFMANN & KLAUS SCHILDBERGER

Zoologisches Institut, Universität Leipzig

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Game theory predicts that at least some of the behaviour patterns displayed during aggressive encounters are used to assess asymmetries in variables that indicate fighting ability and resource value. Game theoretical models such as the sequential assessment game see assessment as the major activity during a fight. However, while these models acknowledge the existence of physical and motivational assessment parameters, there are only a few examples where a mechanism for the assessment of fighting readiness has been shown. In staged encounters between male Mediterranean field crickets, *Gryllus bimaculatus*, fighting behaviour follows a stereotyped escalation cascade with ritualized displays in the beginning and physical combat towards the end. Despite their larger size, heavier animals lost 30% of the encounters even if weight asymmetry was large. To examine whether the contestants provide assessment cues that might explain this surprising result, we analysed two stereotyped displays in detail (antennal fencing and mandible spreading). The duration of antennal fencing, which is necessary to initiate a fight, was independent of experience and weight asymmetry between the contestants, but was prolonged after shortening the antennae by almost 90%. Fights escalated only when antennal movement frequencies were high in both contestants. In blinded crickets few contests were settled by another ritualized display, mandible spreading, and fights that escalated beyond this stage were significantly shorter than in untreated crickets. We suggest that antennal fencing may be used to assess fighting readiness of the opponent, while mandible spreading may indicate fighting ability. We conclude that high willingness to fight may help crickets to overcome inferior fighting ability.

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Over the last quarter of a century, fighting behaviour has been studied extensively from an evolutionary point of view using evolutionary game theory (Maynard Smith 1982a). The war of attrition as well as the hawk–dove game are the two models that have provided the basis for understanding how nonstrategic factors like fighting ability can shape the evolution of fighting behaviour. Parker (1974) designed an animal contest model that utilized ‘conventional fighting’ (Maynard Smith 1972) for assessment of ‘resource holding power’ (RHP). Although a number of important predictions have been made from these early models, they are not based on realistic behavioural mechanisms (i.e. they do not take into account the existence of escalating sequences of behaviour as a result of external and internal signals).

Correspondence and present address: Dr Hans A. Hofmann, Department of Psychology, Jordan Hall, Building 420, Stanford University, Stanford, CA 94305, U.S.A. (email: hans@psych.stanford.edu). Dr K. Schildberger is at the Universität Leipzig, Institut für Zoologie, Talstrasse 33, D-04103 Leipzig, Germany.

**Dedicated to Franz Huber, Seewiesen, Germany, on the occasion of his 75th birthday.*

The observation that threat displays are ubiquitous has been a longstanding puzzle in the understanding of animal conflict (Tinbergen 1953; Andersson 1980). Displays may transmit information about fighting ability, but may also serve other functions. For example, they could signal aggressive motivation and intentions, or contain specific contextual information (Tinbergen 1953). Classical ethologists saw cooperation as the basis for honest signals that are performed at a ‘typical intensity’ (Morris 1957) and become ritualized during the process of ‘adaptive formalization’ (Huxley 1966). This evolutionary process was believed to result in an optimal signal form that minimizes distortion during propagation between sender and receiver. Zahavi (1975) proposed that stereotyped displays are used to compare important qualities that are not easily measured by direct assessment. There are many examples where direct assessment has been shown (e.g. Andersson 1976; Davies & Halliday 1978; Clutton-Brock & Albon 1979; Turner & Huntingford 1986). However, such stereotypy may preclude the extraction of honest information about the sender, an interpretation put forward by behavioural

ecologists who assert that animals may benefit from concealing information about their fighting ability and the value of a resource they might be holding (Dawkins 1976; Krebs & Dawkins 1984). Originally, it was also believed that honest signals, especially if they are energetically cheap and not a direct indicator of RHP, would be vulnerable to cheating and thus could not be evolutionarily stable (Maynard Smith 1982a). However, we now know that a signal does not always have to be costly to be reliable and evolutionarily stable (Maynard Smith 1994; Johnstone 1998).

Should animals communicate information about their intentions to enter or continue a fight (Maynard Smith 1982b; Moynihan 1982)? The sequential assessment game (Enquist & Leimar 1983, 1987) showed that assessment of fighting ability and resource value in animal contests can be evolutionarily stable, and displays may serve specific functions. It seems now that the assessment of intentions is compatible with an adaptive interpretation of motivation (an animal's willingness to fight). That is, animals can be expected to assess each other's motivational states during interactions, and on the basis of that information, in conjunction with assessment of strength, they decide whether to escalate or give up. Probing and retaliation would keep the levels of 'bluffing' about intentions low (Maynard Smith & Parker 1976; van Rhijn 1980; Hazlett 1982). While there are many studies of signals that allow assessment of fighting ability or strength, signals that convey information about resource value and/or motivation (e.g. Wagner 1989; Neat et al. 1998; Kotiaho et al. 1999) have received much less attention.

Male Mediterranean field crickets, *Gryllus bimaculatus*, compete for territorial shelters and females (Shuvalov & Popov 1973; Simmons 1986a), and their aggressive behaviour has been described extensively in the ethological literature (Simmons 1986a; Adamo & Hoy 1995; Hofmann & Stevenson 2000). Although crickets can perform a number of different behaviours during agonistic interactions (Hack 1997; Hofmann 1997), the actual fighting behaviour can be characterized as an escalating fixed-sequence contest: while the sequence can be repeated and sometimes interrupted by bouts of rivalry song, displays are performed mutually and the actual behavioural repertoire used is rather small. Other displays may be used in different contexts (e.g. the maintenance of an established rank order or a situation where one sensory channel cannot be used). For example, it has been shown that song production can be an important social communication tool in male cricket encounters (Heiligenberg 1966; Phillips & Konishi 1973; Hissmann 1991; Hofmann 1997). In addition, pheromones allow sex recognition (Rence & Loher 1977; Tregenza & Wedell 1997). In this paper, we examine the role of two display behaviours, antennal fencing and mandible spreading, as parts of an assessment sequence that occurs during fights between male crickets. We suggest that antennal fencing is an energetically 'cheap' signal that carries mostly motivational information about resource value, whereas mandible spreading indicates strength. These findings give rise to

the notion that subtle differences in the intensity of apparently stereotyped signals, which are not easily detected by human eyes, may convey information relevant for assessment.

METHODS

Experimental Animals

Adult male Mediterranean field crickets, *G. bimaculatus* De Geer, derived from a wild-caught stock were kept physically isolated under constant conditions (24 °C; 40% RH; 12:12 h light:dark cycle) and fed every morning with carrots, apples and lettuce ad libitum (cf. Staudacher & Schildberger 1998). All work was in compliance with the Animal Care and Use Guidelines of Leipzig University.

We weighed age-matched pairs of adult male crickets (weight range 0.68–2.04 g, average 1.30 ± 0.23 g) and placed them in a sand-covered small Plexiglas glass arena (16 × 9 cm) with two compartments separated by a removable divider. After removal of the divider, animals usually started fighting immediately. In rare cases (ca. five fights) where the animals did not face each other, we coaxed them by stroking the cerci and antennae with a hair brush until they turned around. Although in some cases we reused animals the day or several days after their initial fight, this did not bias our results, because 24 h after a fight male crickets engage like naïve animals (Hofmann & Stevenson 2000). In cases where fights were not videotaped (see below) we measured fight duration to the nearest second with a stopwatch. To control for possible fluctuations of aggressiveness in a 24-h day, we conducted experiments between 0800 and 1100 hours. At this time of day, less than 20% of males were in possession of a spermatophore (cf. Loher 1989), and fight outcome was independent of the presence of a spermatophore.

All crickets were between 2 and 4 weeks old, because animals younger than 1 week and older than 6 weeks are significantly less aggressive (unpublished observations). We calculated weight asymmetry as the logarithm of the weight ratio (weight of heavier individual/weight of lighter individual) according to Enquist et al. (1990). For example, a weight asymmetry of 0.31 corresponds to a difference in weight of 38%. Weight is highly correlated with body length (linear regression: $Y=11.73X+14.75$; $r^2=0.82$; regression ANOVA: $F_{1,18}=82.36$, $P<0.0001$), pronotum width ($Y=2.04X+6.0$; $r^2=0.73$; $F_{1,18}=56.81$, $P<0.0001$) and head width ($Y=2.75X+4.34$; $r^2=0.73$; $F_{1,18}=48.65$, $P<0.0001$). Daily individual fluctuations of weight, and consequently of condition, were small ($\leq 8\%$). From this we concluded that weight is a good indicator of both size and strength (cf. Simmons 1986a; Marden & Waage 1990).

In some experiments we removed one or both flagella of the antennae completely or shortened them to one-half (10–15 mm) or one-eighth (3–4 mm) of their original length. In these cases, we paired all crickets with weight-matched partners that had undergone the same treatment and we staged fights at least 24 h after the surgery.

In another experiment we blinded the crickets by applying black enamel (Faber Castell, Nürnberg, Germany) to their eyes. We verified the effectiveness of the blinding by stimulating the animals with a quickly approaching black object while they were in the Plexiglas arena (to prevent air movement). Blinded animals did not respond to this stimulus, whereas crickets with their eyes intact responded with escape behaviour. To assure proper blindfolding, we painted the animals' eyes only a few hours before the experiment.

Video Analysis of Staged Fights

Most of the fights presented in this paper were filmed from the side and from above with a CCD colour video camera (Model DXC-151P, Sony) and recorded on a video-cassette recorder (U-matic VO-7630, Sony). Two consumer-grade halogen lamps were used as light source. We determined duration and frequency of all components of fighting behaviour by replaying the tapes on a colour video monitor (Trinitron PVM-1442QM, Sony). To assess the sampling error of this technique some sequences were analysed repeatedly by the same person or by several persons. This procedure revealed that the duration of single behavioural components could be measured with an accuracy of 0.1 s (equivalent to five video frames in PAL standard: Phase Alternation Line: 25 frames/s; resolution 50 kHz), with almost no detectable error in the frequency of components.

High-speed Film Analysis of Antennal Movements

Video analysis revealed that in most cases the oscillation frequencies during antennal fencing could not be resolved with the standard PAL video rate of 50 Hz. Preliminary data obtained with a linear CCD array (courtesy of Hans-Ulrich Kleindienst, Seewiesen, Germany) indicated that frequencies greater than 50 Hz were rare and small in amplitude. Therefore, we decided to record bouts of antennal fencing during aggressive encounters with a 16-mm high-speed camera (Loccum) at 200 frames/s on appropriate high-speed film (RAR Film 2479, Kodak, Stuttgart, Germany). A consumer-grade halogen lamp was used as light source.

The maximal duration of one recording session at the chosen speed (200 frames/s) was limited by the film length (ca. 20 s for 38-m film). High spatial resolution was necessary to visualize the thin antennae (diameter ca. 1–2 mm). Therefore, we placed two crickets on a 2 cm wide gangway mounted on a vehicle built with Duplo[®] building blocks (Lego, Billund, Denmark). Seconds before the two animals began to interact, we turned on the camera and slowly moved the gangway vehicle such that the combatants were in front of a 5 × 5 cm measuring window at a fixed distance from the camera.

The exposed films were developed (Andec Filmtechnik, Berlin) and copied frame by frame on VHS videotapes (Witt Filmgesellschaft, Berlin) for further analysis. We digitized sequences of interest and determined the coordinates of the antennal base and of a point 10 mm

distal from the base of the antenna for the two pairs of antennae using image processing software (Heinz Bendele, Universität Tübingen). We calculated the angular elevation over the azimuth (in degrees) from the raw data (Microsoft Excel). We plotted these values over time and, after Fast Fourier Transformation with a standard algorithm (Igor Pro, Wave Metrics), in the frequency domain as amplitude spectra. In all cases where the antennal fencing sequences were of sufficient length to digitize the antennal trajectories continuously for at least 1 s (6 of 14 recorded sequences), the frequency distribution was multimodal with the maxima of the first two or three modes exceeding 7°. We determined the centres between successive amplitude maxima as start and end points of the distribution around the highest frequency mode that exceeded this threshold, and calculated the mean of this mode. Finally, we calculated the frequency ratio R_f between the maximal frequencies f_{\max} for both antennae of loser and winner as $R_f = f_{\max}(\text{winner})/f_{\max}(\text{loser})$.

Statistics

We calculated means and standard deviations for normally distributed metric data. We performed analysis of variance (ANOVA) for the comparison of multiple distributions. We used Kruskal–Wallis test for multiple comparisons of ordinal data. We applied Student's *t* test or complementary tests for nonparametric and ordinal data where appropriate for calculating the differences between two independent samples. We regarded results as significantly different from the null hypothesis when $P < 0.05$. We performed all statistical calculations with GB-STAT software (Dynamic Microsystems, Silver Spring, Maryland, U.S.A.).

RESULTS

The Structure of a Cricket Fight

Fighting crickets display a stereotyped sequence of escalating motor behaviours. We divided this escalation cascade into the following levels of aggression (modified after Alexander 1961; Fig. 1): Level 0: mutual avoidance, no interaction; Level 1: clear dominance, one animal retreats immediately; Level 2: antennal fencing, involving both animals; Level 3: mandible spreading (unilateral), one animal displays spread mandibles; Level 4: mandible spreading (bilateral), both animals display spread mandibles; Level 5: mandible engagement, mandibles make contact and crickets push against each other; Level 6: 'wrestling', an all-out fight where the animals interlock mandibles and push each other. They may repeatedly disengage, struggle for position, bite other body parts, and re-engage mandibles to push the opponent. The fight can be concluded at any of the levels 1–6 by one opponent, the loser, retreating, upon which the established winner typically produces victory displays such as the rivalry song and characteristic body-jerking movements. Most fights escalate to level 5 (median: 5;

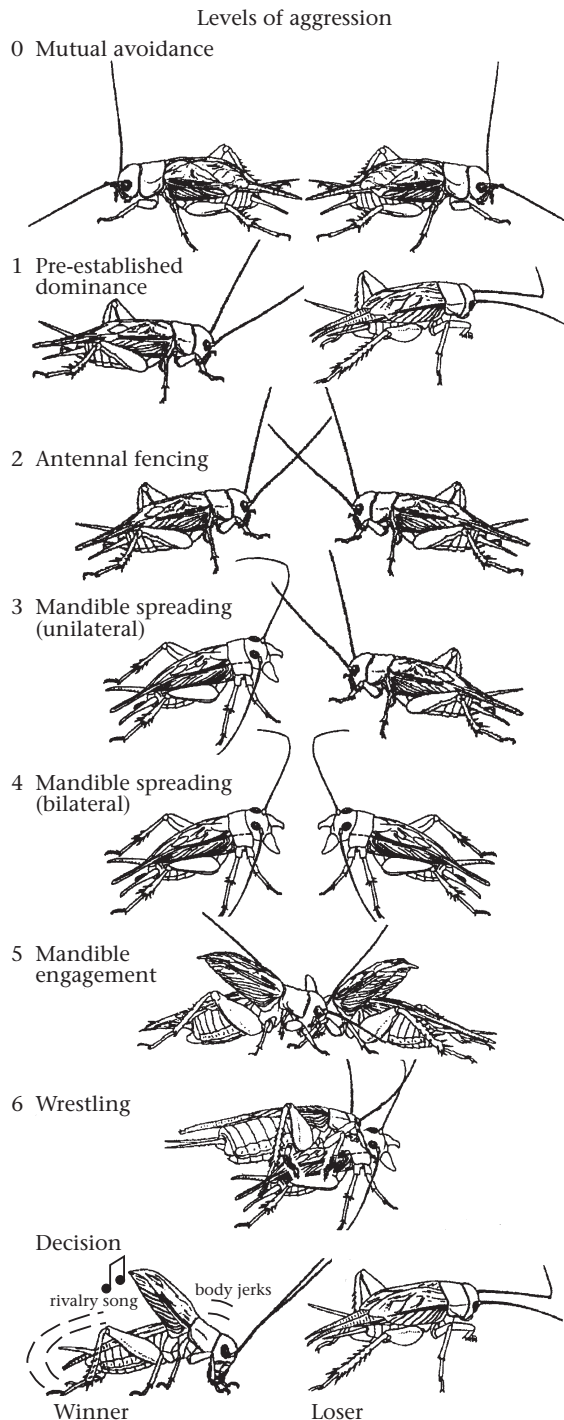
interquartile range 4–6; $N=179$). After defeat, losers usually do not engage in any further aggressive interaction until hours later (Hofmann & Stevenson 2000).

Effect of Weight Asymmetry on Fight Outcome and Duration

Surprisingly, the probability of victory for the heavier animal stabilized around 70% (i.e. even in instances where weight asymmetry was large the smaller animals

won more than 25% of the fights; Fig. 2a). Independent of weight asymmetry, lighter animals won only 29% ($N=22$) and 33% ($N=53$) of Level 3 and Level 4 fights, respectively. In contrast, although not significantly different from Levels 3 and 4, 47% of Level 2 ($N=32$), 38% of Level 5 ($N=63$) and 41% of Level 6 fights ($N=26$) were won by the lighter crickets (chi-square test: $\chi^2_4=3.10$, $P=0.54$).

According to the model put forward by Enquist & Leimar (1983), fight duration (as a measure of cost) and its standard deviation should decrease with increasing weight asymmetry. However, in the present study, average fight duration and its standard deviation were independent of this asymmetry (linear regression: $Y=1.79X+8.16$; $r^2=0.0002$; regression ANOVA: $F_{1,196}=0.04$, $P=0.84$; Fig. 2b). Furthermore, weight asymmetries did not differ significantly between final levels of aggression (ANOVA: $F_{4,191}=0.90$, $P=0.47$; Fig. 2c). Finally, the median level of aggression reached in a fight was also independent of weight asymmetry (Kruskal–Wallis test: $H_{7,191}=0.74$, $P=0.998$).



Stereotypy of Antennal Fencing and Mandible Spreading

Antennal fencing and mandible spreading displays were both remarkably stereotyped and robust across a number of parameters. Although ANOVA of antennal fencing durations yielded significance for aggression levels ($F_{4,205}=3.04$, $P<0.05$), Games–Howell post hoc comparisons showed no significant difference (Fig. 3a). Duration of mandible spreading was significantly shorter only at Level 3 ($F_{3,165}=4.05$, $P<0.01$; Games–Howell post hoc comparisons: $P<0.05$; Fig. 3b). As mentioned above, mandible spreading in Level 3 contests corresponds to a unilateral display that is immediately followed by the retreat of the nondisplaying animal. When the same individuals were paired once every day, neither antennal fencing (Spearman rank correlation: $r_s = -0.22$, $N=15$, $P=0.43$) nor mandible spreading ($r_s = -0.23$, $N=15$, $P=0.41$) displayed changes in duration with increasing number of interactions (Fig. 3). Finally, both

Figure 1. Pictogram illustrating the stereotyped escalating sequence of motor performances (Level 0–6) characteristic for aggressive encounters between male crickets (modified from Alexander 1961). Level 0: mutual avoidance: no aggressive interaction. Level 1: pre-established dominance: one cricket attacks, the other retreats. Level 2: antennal fencing: the two crickets lash with their antennae. Level 3: mandible spreading (unilateral): one cricket displays broadly spread mandibles. Level 4: mandible spreading (bilateral): both crickets displays their spread mandibles. Level 5: mandible engagement: the mandibles interlock and the animals push against each other. Level 6: wrestling: an all-out fight where the animals may repeatedly disengage, struggle for position, bite other body parts, and re-engage mandibles to push the opponent. Decision: the fight can be concluded at any of the Levels 1–6 by one opponent, the loser, retreating, upon which the established winner typically produces the rivalry song together with characteristic body-jerking movements. (Sketches of crickets adopted in part from Stevenson et al. 2000.)

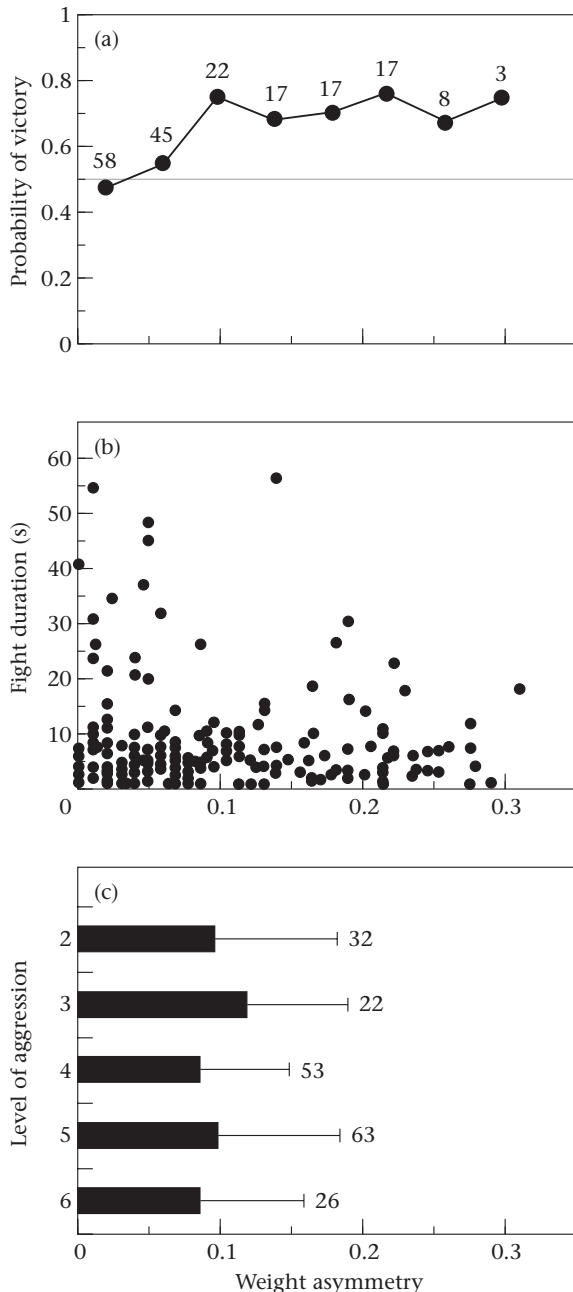


Figure 2. Influence of weight asymmetry on cricket fights. (a) When the weight difference was large, the heavier animal was more likely to win an encounter. However, the probability of victory stabilized around 70% even when weight asymmetry was large. All weight asymmetries were grouped in bins 0.04 units wide. Numbers indicate sample sizes. Note that this analysis does not include fights where weight asymmetry was 0 ($N=10$). (b) Fight duration and (c) final levels of aggression (mean \pm SD) were independent of weight asymmetry. Note that there was only one Level 1 encounter.

display durations were independent of weight asymmetry between the contestants (antennal fencing: linear regression: $Y=0.81X+1.88$; $r^2=0.003$; regression ANOVA: $F_{1,197}=0.67$, $P=0.41$; Fig. 3a; mandible spreading: $Y=2.12X+2.37$; $r^2=0.01$; $F_{1,160}=1.88$, $P=0.17$; Fig. 3b).

However, when we analysed mandible spreading in Level 4 fights separately we found a significant increase in display duration with weight asymmetry ($Y=11.99X+1.78$; $r^2=0.20$; $F_{1,51}=13.10$, $P<0.001$).

The Role of the Antennae

Crickets begin their fights with antennal contact followed immediately by antennal fencing. When the flagella of both antennae were removed fights did not occur (Fig. 4a), even if two previously dominant animals were paired. Instead, in more than 50% of all cases, either one or both animals carried out courtship behaviour (courtship song and mounting attempts). In intact animals, in those with only one flagellum, and in those with both flagella shortened to 14–15 mm (ca. half of their original length), we never observed courtship behaviour. In all other interactions between animals without flagella, one animal retreated immediately after initial contact with the palpi or other parts of the body, while its rival showed all elements of dominance (mandible spreading, chasing, body jerks, rivalry song); that is, aggression per se was not abolished by the surgery. Animals with both flagella shortened to 3–4 mm (ca. one-eighth of original length) performed somewhat intermediately. Approximately 50% of the interactions were fights, 30% courtship and 20% showed clear dominance. Interestingly, the duration of antennal fencing in animals with very short flagella was significantly longer (ANOVA: $F_{3,129}=10.35$, $P<0.0001$; post hoc comparisons after Games–Howell: $P<0.01$; Fig. 4b). Once a fight had been initiated, the subsequent escalation stage (mandible spreading) did not differ in duration between test groups and controls (ANOVA: $F_{3,117}=1.66$, $P=0.18$). Neither did the level of aggression that was ultimately reached (Kruskal–Wallis test: $H_{3,128}=5.44$, $P=0.14$) nor the total duration of the fights (ANOVA: $F_{3,135}=2.50$, $P=0.06$) differ.

The Frequency of Antennal Fencing as an Assessment Parameter

Besides duration of a particular display and its repetition, the frequency of antennal movements could contain information about an animal's fighting ability and/or readiness. We analysed the frequency of these movements during the initial bout of antennal fencing. Of the 14 recorded antennal fencing sequences, six were of sufficient length to digitize the antennal trajectories continuously for at least 1 s. Crickets can move each antenna independently from the other (Honegger 1981) and do this to a large extent even during intense antennal fencing bouts (Figs 5a, 6a). Often, one antenna may perform only slow scanning movements while the other lashes with a rather constant frequency (see 'Winner' in Fig. 5 as a representative example). When the antennal frequency spectra of two displaying animals were compared with each other as well as with the level of aggression to which each fight escalated, a very clear correlation emerged: animals whose maximal antennal frequencies

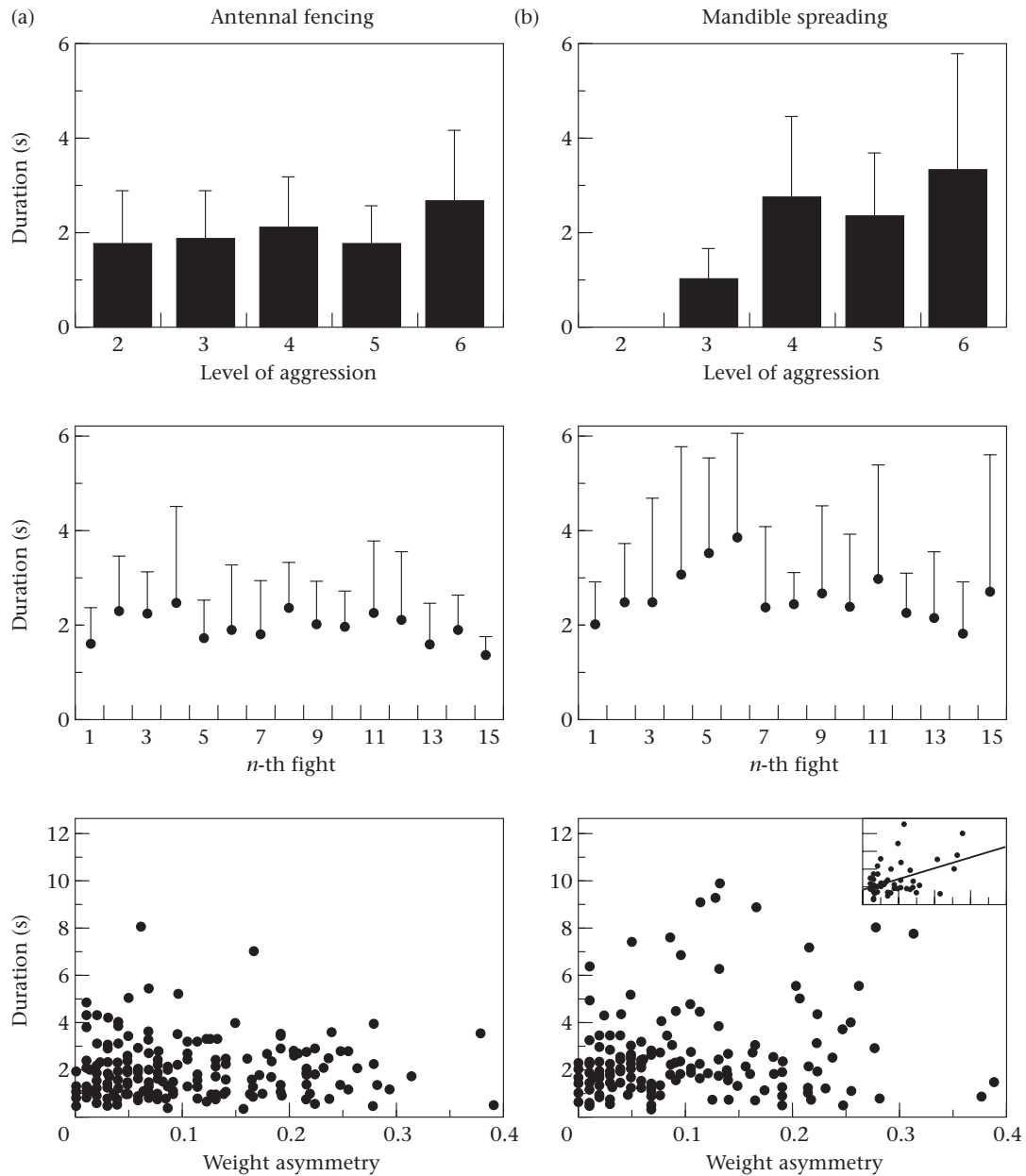


Figure 3. Stereotypy of aggressive displays during cricket fights. Duration of both antennal fencing (a) and mandible spreading (b) was independent of the aggression level an encounter reached (top graphs). When the same animals were paired daily for 15 consecutive days, neither antennal fencing nor mandible spreading changed significantly in duration (centre graphs). The duration of these displays was also independent of weight asymmetry (bottom graphs). However, mandible spreading duration during Level 4 fights increased with weight asymmetry (inset).

differed only slightly during the antennal fencing phase of their encounter (Fig. 5b) escalated to a physical combat. Conversely, opponents whose maximal frequencies differed greatly (Fig. 6b) settled their conflicts immediately. Interestingly, the maximal frequency (defined as the mean of the highest frequency mode exceeding 7°; see Methods) varied considerably between animals and even in the same individual between consecutive fights (data not shown). Post hoc separation of the frequency ratios R_f into nonescalating and escalating fights (Fig. 7a) resulted in a significant difference between the mean R_f values (unpaired t test: $t_2=4.69$, $P<0.02$). In addition, the mean

R_f value of escalating fights did not differ significantly from 1 (i.e. $f_{\max}(\text{winner})=f_{\max}(\text{loser})$; one-sample t test: $t_2=1.94$, $P=0.19$). As shown in Fig. 7b, aggression levels of the fights were inversely correlated with the frequency ratio (Spearman rank correlation: $r_s=-0.88$, $N=6$, $P<0.02$).

Mandible Spreading as a Visual Assessment Parameter

Blinded crickets escalated more fights to Levels 5 and 6 than did untreated crickets. While the frequency of fights

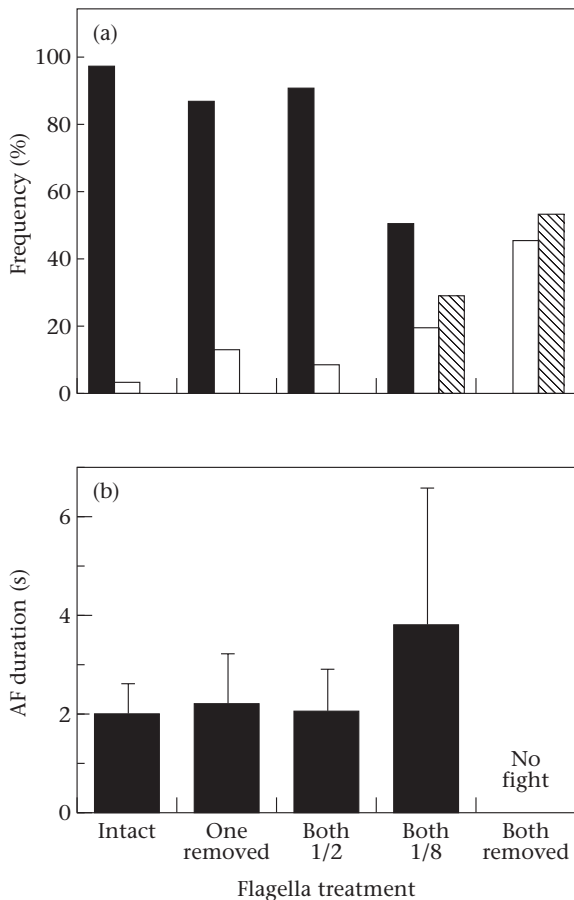


Figure 4. Effects of antennal manipulations on aggressive behaviour. (a) Crickets whose antennal flagella were reduced to one-eighth of their original lengths (both shortened; $N=39$ encounters) or removed completely (both removed; $N=39$) showed increasingly either subordinate (Level 0, \square) or courtship behaviour (\boxtimes). Fighting behaviour (\blacksquare) occurred with normal frequency (untreated; $N=38$) as long as only one flagellum was removed ($N=38$), or both flagella were still 50% of their original length ($N=24$). An interaction was counted as pre-established dominance (Level 0) if one animal retreated directly after a contact and the other showed some kind of dominance behaviour like mandible spreading, chasing, body jerks or rivalry song. An interaction was counted as courtship if one or both animals sang the courtship song and did not switch to fight or escape behaviour within 1 min. Interactions were counted as fights if the aggression exceeded Level 3, that is, both animals clearly showed fight elements (4×3 contingency table: $\chi^2_8=81.9168$, $P<0.0001$). (b) Mean duration (\pm SD) of antennal fencing (AF) significantly increased in crickets whose antennae were reduced to one-eighth of their original length.

with mandible spreading as the final stage (Levels 3 and 4) dropped sharply compared with intact controls, the number of Level 5 fights increased greatly (Fig. 8a). The two distributions differed significantly (Kolmogorov–Smirnov test: $KS-Z=3.24$, $P<0.0001$). Most of the Level 5 encounters between blinded crickets were short compared with those of the control group (Fig. 8b). The average duration of Level 5 fights dropped from 7.55 ± 2.35 s, $N=49$, in intact animals to 5.14 ± 1.71 s,

$N=49$, in blinded crickets (t test: $t_{96}=5.79$, $P<0.0001$). There was a similar, yet nonsignificant tendency for the duration of Level 6 fights to decline (intact: $\bar{X} \pm SD=31.51 \pm 16.97$ s, $N=30$; blinded: $\bar{X} \pm SD=23.00 \pm 14.41$ s, $N=23$; t test: $t_{51}=1.93$, $P=0.06$).

DISCUSSION

The aim of the experiments presented here was to discover which cues male crickets use for the assessment of an opponent's strength and willingness to fight during agonistic encounters. In the following discussion we will interpret our results in the context of existing theoretical models of animal conflict. Given our surprising discovery, in contradiction to Enquist & Leimar (1983), that weight asymmetry is not a very reliable predictor of outcome, duration, or intensity of staged fights between isolated crickets, this raises the question of whether and how crickets can compensate for smaller size during a fight.

The sequential assessment game (Enquist & Leimar 1983, 1987) predicts that fight duration (as a measure of cost) and its standard deviation should decrease with increasing weight asymmetry. The finding that even when weight asymmetry is large, the lighter animal wins more than 30% of all fights indicates that cues other than strength (as measured by weight) are important during escalated fighting in crickets. While we do not know the nature of these cues, we can hypothesize that aside from 'chance' and unpredictable external influences, high fighting readiness may allow even markedly smaller animals to succeed in such fights. If this is the case, we would expect assessment of willingness to fight to be as important as the assessment of strength (i.e. RHP sensu Maynard Smith 1982; Parker 1974). Parker (1974) noted that 'escalations should be restricted to closely matched RHP opponents if RHP is the major imbalance'. Clearly, other asymmetries must play a role in cricket contests, and an asymmetry in willingness to fight coupled with an inverse asymmetry in RHP may allow a smaller animal to dominate in a situation where weight asymmetry is large.

As we have shown, both antennal fencing and mandible spreading are very robust and stereotypical displays. The duration of these phases is independent of weight asymmetry as well as fight duration and level of aggression, which is in agreement with the sequential assessment game (Enquist & Leimar 1983). When confronted with an opponent, a cricket must acquire appropriate information about its opponent prior to initiating a fight. A cricket acquires this information using its antennae, and the flagellum of one antenna is sufficient. Short flagella acquire information less reliably, which is compensated for by a longer duration of antennal fencing. If proper recognition is not possible because of a lack of antennal input, the animals behave subordinatesly or court the other male. Our results suggest that crickets may be able to assess relative fencing frequency, most likely by means of antennal mechanoreceptors. Because antennal fencing seems to be an energetically inexpensive signal that is not necessarily correlated with the strength of an animal, we propose that it is used mostly

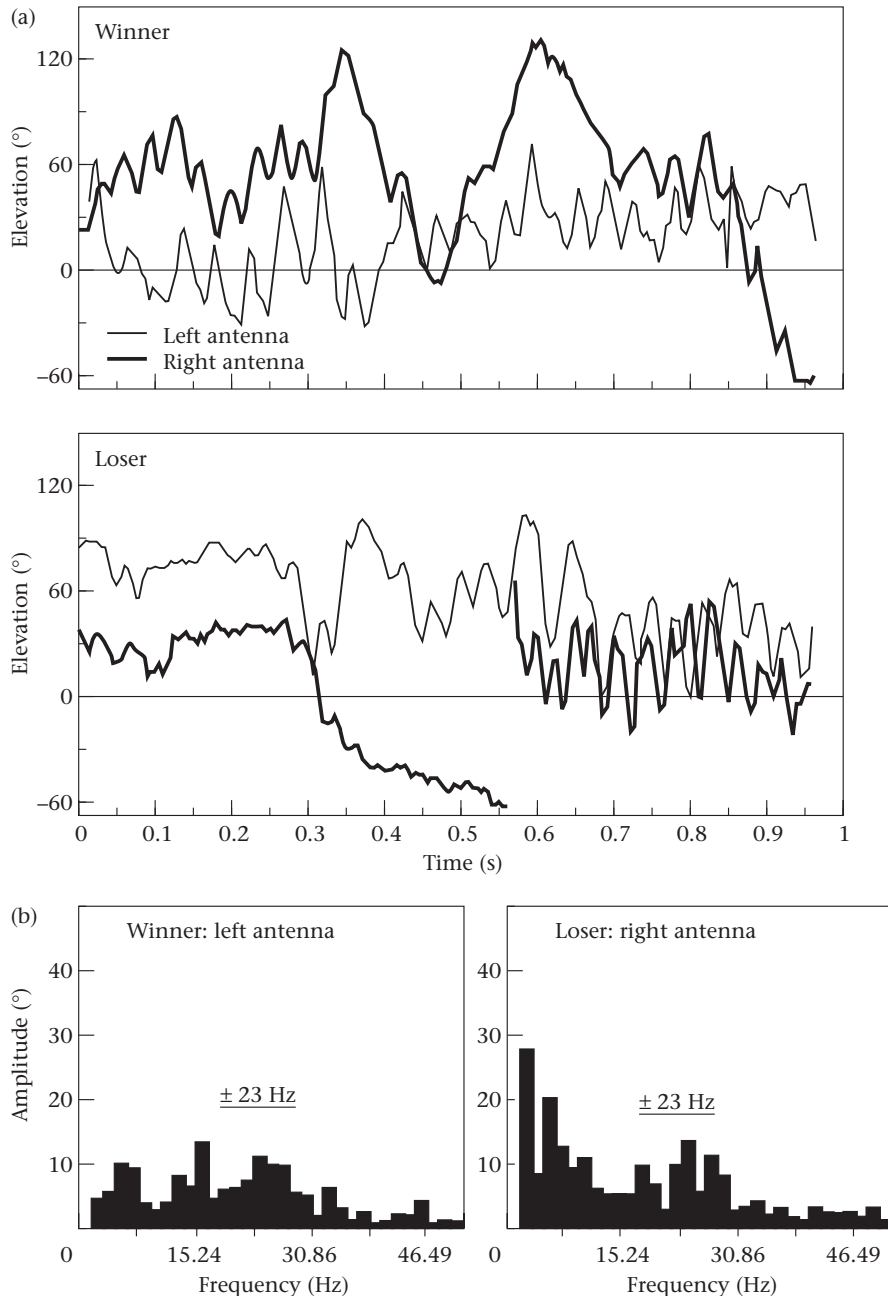


Figure 5. Analysis of antennal fencing at the beginning of a Level 5 fight. (a) Elevation of left and right antennae over time. (b) Frequency spectra of antennal movements of both animals. The spectrum shown for each animal is from the respective left and right antenna, which showed the highest frequencies according to the criterion (see Methods). Note that both animals had very similar frequency maxima around 23 Hz.

to gain information about the opponent's willingness to escalate.

Enquist (1985) and Enquist et al. (1998) predicted that inexpensive signals of motivation will be discrete even if motivation varies continuously. While antennal fencing may be continuous in its information content, crickets may perceive this signal as discrete due to low sensory resolution. Clearly, cheap signals may invite cheating and the possibility of bluff must be considered (Parker 1974), that is, antennal fencing might not be an evolutionarily stable parameter for the assessment of the willingness to

fight (Maynard Smith 1982a; but see Maynard Smith 1994). Because of the possibility of cheating, antennal fencing may after all signal an animal's overall condition, especially in older crickets (similar to roaring in red deer, Clutton-Brock & Albon 1979). However, although the necessary costs for antennal fencing (predation risk, energy and lost time) are low, its incidental costs (probing in the form of dangerous fighting) are high and may keep cheating under control. While the next stage of escalation in cricket fights, mandible spreading, may not represent such potentially dangerous probing, it is clear from our

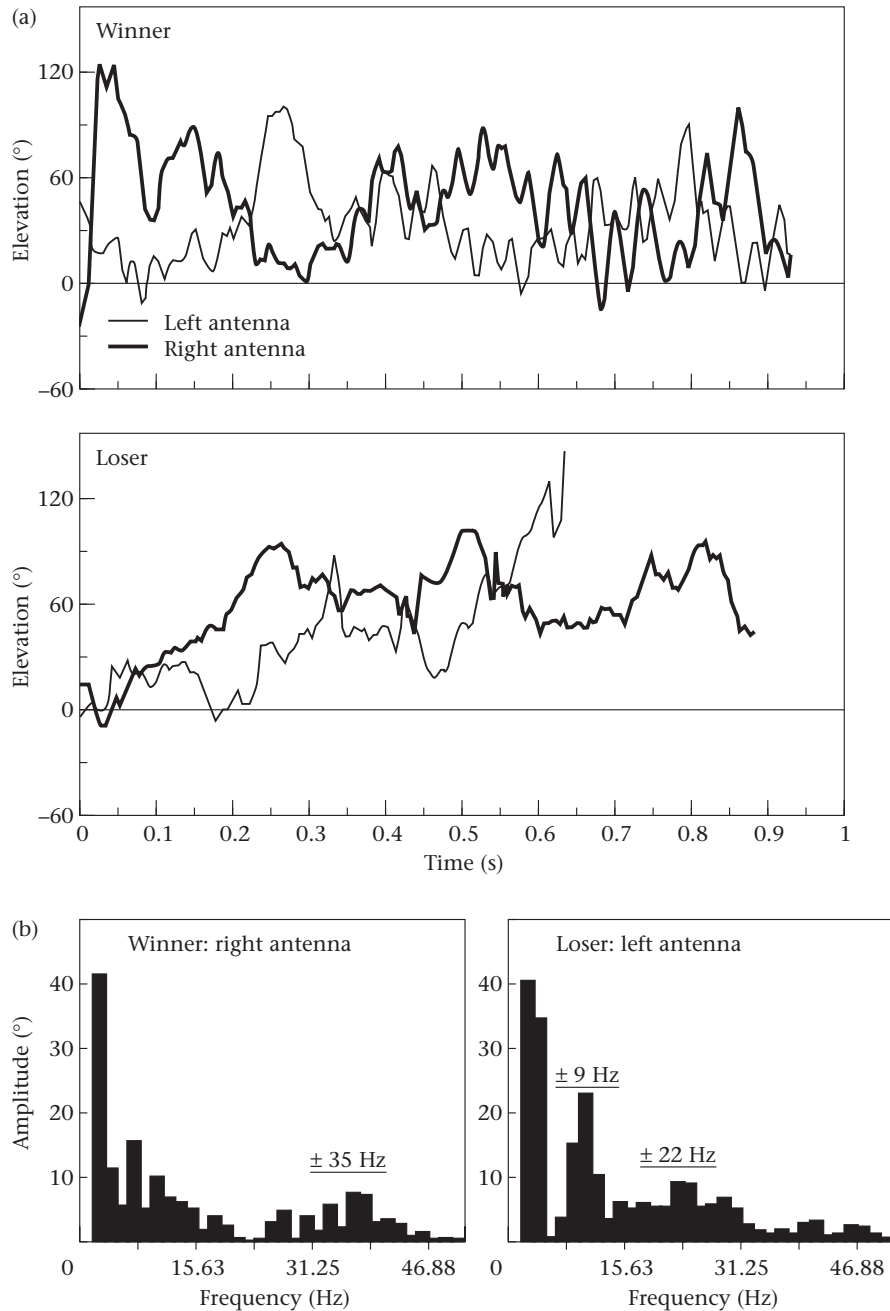


Figure 6. Analysis of antennal fencing at the beginning of a Level 3 encounter. (a) Elevation of left and right antennae over time. (b) Frequency spectra of antennal movements of both animals. The spectrum shown for each animal is from the respective right and left antenna, which showed the highest frequencies according to the criterion (see Methods). Note that the frequency maximum of the winner (35 Hz) was more than 50% greater than the maximum displayed by the loser (22 Hz).

experiments with blinded crickets that an opponent will omit this step if assessment is not possible. Because natural light conditions are not always sufficient (assuming that mandible spreading provides visual information about the size and strength of the opponent), a cricket can never be sure that a contest will be settled by nondangerous mandible spreading. Even then the winner violently chases the loser away. We do not yet know the extent to which cheating takes place and whether larger animals retreat after antennal fencing (47% of Level 2

contests were won by the smaller animal) because of their relatively lower willingness to fight. However, if this willingness is positively correlated with resource value, a larger animal may decide to escalate against a highly motivated smaller cricket only if it is highly motivated itself to take possession of the contested resource.

Resource value, apart from fighting ability, is likely to be the most important nonstrategic variable in fighting behaviour. For example, [Austad \(1983\)](#) has shown that resource value will determine fight duration in the bowl

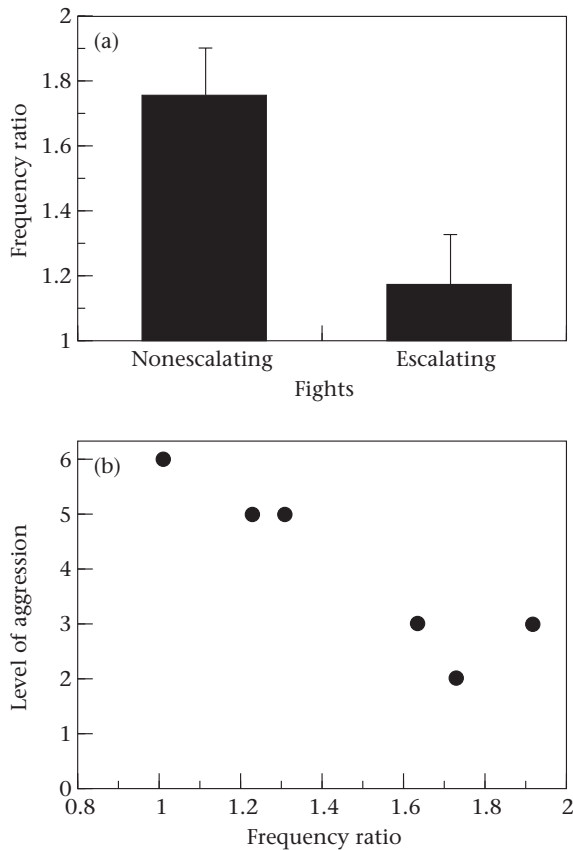


Figure 7. Statistical evaluation of frequency differences found during antennal fencing. (a) The mean ratio of the maximal frequencies ($R_f = f_{\max}(\text{winner})/f_{\max}(\text{loser})$) in nonescalating fights (Levels 2 and 3; $R_f = 1.75 \pm 0.15$) was significantly higher than in escalating fights (Levels 4–6; $R_f = 1.17 \pm 0.16$). (b) The level of aggression reached in an encounter was highly correlated with the ratio of maximal frequencies reached during antennal fencing.

and doily spider, *Frontinella pyramitela*. In this species, the holder of a resource that has lost value will not escalate against an intruder but retreat after a brief interaction. Resource value can therefore be interpreted as one important determinant of the willingness to fight. Among male crickets, the most important resources are territories and females. When population density decreases, chance encounters between males and females become less likely and calling territorial males attract more mates (Hissmann 1991). Under these conditions, the value of a territory, and with it the willingness to defend it, may increase considerably. After mating, the male guards the female aggressively, which may prevent access of other males and secure repeated matings while a new spermatophore is being produced (Simmons 1986b). Loher (1989) suggested that in *G. bimaculatus*, where formation of a new spermatophore is slow (ca. 60 min), mate guarding assures that the female's eggs become fertilized before she can remove the spermatophore and/or before another male attempts to mate (Loher & Rence 1978). As a consequence, the female would lose value as time passes.

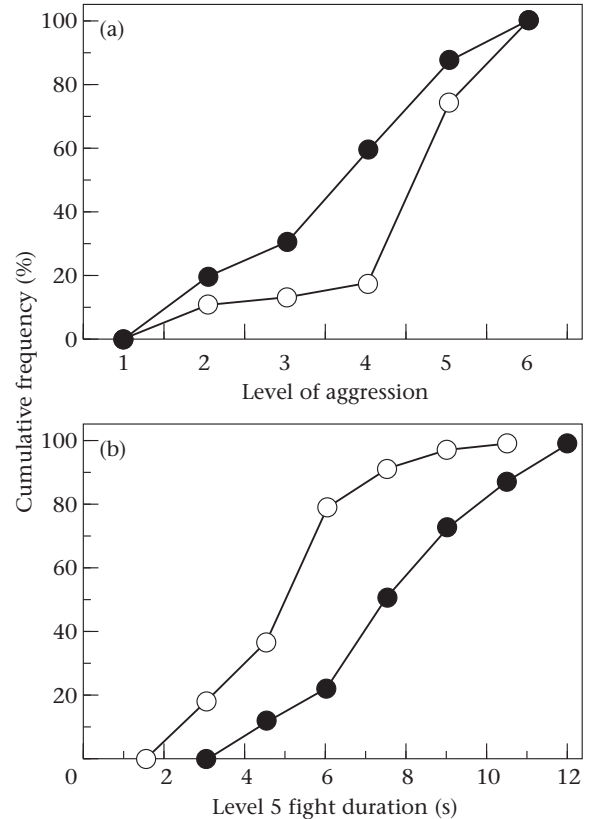


Figure 8. Blinded crickets escalated to higher levels of aggression. (a) The cumulative relative frequency plot of aggression levels shows that in blinded animals (○; $N=88$ encounters), Level 3 and Level 4 encounters (where mandible spreading was the final display) occurred much less frequently than in untreated controls (●; $N=179$). The proportion of Level 5 and Level 6 fights, however, markedly increased in this condition. (b) Cumulative relative frequency plot of Level 5 fight duration. Although blinded animals escalated more often to Level 5, the duration of these fights was significantly shorter than in untreated animals.

High motivation enables animals to dominate over relatively larger opponents (Wagner 1989; Neat et al. 1998; Kotiaho et al. 1999). However, it is a dynamic factor: a cricket at the end of its reproductive phase may be much more likely than an animal early in its life to defend a suboptimal territory against an intruder with escalated fighting. While potentially less accurate in populations with many age cohorts, assessment of the willingness to fight as a measure of resource value via antennal fencing may provide reliable information in crickets. If this is the case, it is clear why an intruder, who has less information about the current value of the resource than its holder, should try to assess this variable. It also seems beneficial for a resident territorial male to reveal its willingness to defend the resource because it may reduce the risk of escalated fighting and predation (cf. Davies 1981). It is interesting, however, that fighting readiness could be such an asymmetric variable in staged contests between isolated age-matched animals for which the resource value should be the same. However, as demonstrated by Neat et al. (1998), asymmetries in

internal factors like gonadal status can bias fight motivation and outcome to a great extent. In the present study, experiments were carried out in the morning, and thus at a time when most males do not possess a spermatophore (Loher 1989). However, the potential role of the spermatophore should be further explored, especially since at the onset of the calling period at dusk almost every male holds a spermatophore (Loher 1989).

What is the evidence that mandible spreading serves as an assessment cue for strength? First, the duration of mandible spreading was significantly shorter in Level 3 encounters. When a contestant's decision to continue beyond the antennal fencing stage is 'borderline', it needs only a very short time for visual assessment if the opponent's mandibles are clearly bigger (presumably indicating superior strength). This interpretation is supported by the trend that smaller animals won a smaller portion of fights that terminated with mandible spreading (Levels 3 and 4) compared with either Level 2 or Levels 5 and 6 contests. Second, the increase in mandible spreading duration with weight asymmetry during Level 4 fights could result from a conflict in the smaller contestant between high aggressive readiness and relatively little strength (as assessed by mandible size). Such an animal may have to probe longer before it can make a decision as to whether it should continue the fight or retreat. Third, although encounters between blinded animals that escalated beyond Level 2 were rarely decided without physical engagement (Levels 5 and 6), these physical engagements were brief, presumably because an inferior animal with only average fighting readiness can readily assess its own fighting ability relative to that of its opponent. In the field, situations may occur when assessment of relative strength by mandible spreading is not possible. For example, *G. bimaculatus* becomes active at dusk, and thus mandible spreading as a visual display may not always yield reliable assessment. According to our results we would expect that some of the encounters may escalate to Levels 5 or 6 because of a lack of visual assessment cues, but are decided more quickly than is the case in daylight.

Assessment of an opponent's RHP by means of direct and honest indicators such as size is an important feature of many animal contests. Because of the possibility of cheating, it is much more difficult to show that individuals also provide reliable information on their willingness to begin and/or continue a fight using cheap signals such as antennal fencing in crickets. However, such a signal may be evolutionarily stable as long as both opponents benefit from its use. Behavioural and physiological analysis with high temporal and spatial resolution of contests between animals whose individual life histories are known in detail should provide the information necessary to answer these questions.

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References

- Adamo, S. A. & Hoy, R. R. 1995. Agonistic behaviour in male and female field crickets, *Gryllus bimaculatus*, and how behavioural context influences its expression. *Animal Behaviour*, **49**, 1491–1501.
- Alexander, R. D. 1961. Aggressiveness, territoriality, and sexual behaviour in field crickets (Orthoptera: Gryllidae). *Behaviour*, **17**, 130–223.
- Andersson, M. 1976. Social behaviour and communication in the great skua. *Behaviour*, **58**, 40–77.
- Andersson, M. 1980. Why are there so many threat displays. *Journal of Theoretical Biology*, **86**, 773–781.
- Austad, S. N. 1983. A game theoretical explanation of male combat in the bowl and doily spider (*Frontinella pyramitela*). *Animal Behaviour*, **31**, 59–73.
- Clutton-Brock, T. H. & Albon, S. D. 1979. The roaring of red deer and the evolution of honest advertisement. *Behaviour*, **69**, 145–170.
- Davies, N. B. 1981. Calling as an ownership convention on pied wagtail territories. *Animal Behaviour*, **29**, 529–534.
- Davies, N. B. & Halliday, T. R. 1978. Deep croaks and fighting assessment in toads *Bufo bufo*. *Nature*, **274**, 683–685.
- Dawkins, R. 1976. *The Selfish Gene*. Oxford: Oxford University Press.
- Enquist, M. 1985. Communication during aggressive interactions with particular reference to variation in choice of behaviour. *Animal Behaviour*, **33**, 1152–1161.
- Enquist, M. & Leimar, O. 1983. Evolution of fighting behaviour: decision rules and assessment of relative strength. *Journal of Theoretical Biology*, **102**, 387–410.
- Enquist, M. & Leimar, O. 1987. Evolution of fighting behaviour: the effect of variation in resource value. *Journal of Theoretical Biology*, **127**, 187–205.
- Enquist, M., Ghirlanda, S. & Hurd, P. L. 1998. Discrete conventional signalling of continuously varying resource value. *Animal Behaviour*, **56**, 749–753.
- Enquist, M., Leimar, O., Ljungberg, T., Mallner, Y. & Segerdahl, N. 1990. A test of the sequential assessment game: fighting in the cichlid fish *Nannacara anomala*. *Animal Behaviour*, **40**, 1–14.
- Hack, M. A. 1997. Assessment strategies in the contests of male crickets, *Acheta domesticus* (L.). *Animal Behaviour*, **53**, 733–747.
- Hazlett, B. A. 1982. Resource value and communication strategy in the hermit crab *Pagurus bernhardus* (L.). *Animal Behaviour*, **30**, 135–139.
- Heiligenberg, W. 1966. The stimulation of territorial singing in house crickets (*Acheta domesticus*). *Zeitschrift für vergleichende Physiologie*, **53**, 114–129.
- Hissmann, K. 1991. Phonotaxis of male crickets (*Gryllus campestris*) in a field population as an indication of territoriality (Orthoptera: Gryllidae). *Journal of Insect Behavior*, **4**, 675–681.
- Hofmann, H. A. 1997. Aggression in crickets: function and mechanisms. Ph.D. thesis, University of Leipzig.
- Hofmann, H. A. & Stevenson, P. A. 2000. Flight restores fight in crickets. *Nature*, **403**, 613.
- Honegger, H. W. 1981. A preliminary note on a new optomotor response in crickets: antennal tracking of moving targets. *Journal of Comparative Physiology*, **142**, 419–421.

- Huxley, J. S.** 1966. Ritualization of behaviour in animals and men. *Philosophical Transactions of the Royal Society of London, Series B*, **251**, 249–271.
- Johnstone, R. A.** 1998. Game theory and communication. In: *Game Theory and Animal Behavior* (Ed. by L. A. Dugatkin & H. K. Reeve), pp. 94–117. Oxford: Oxford University Press.
- Kotiaho, J. S., Alatalo, R. V., Mappes, J. & Parri, S.** 1999. Honesty of agonistic signalling and effects of size and motivation asymmetry in contests. *Acta Ethologica*, **2**, 13–21.
- Krebs, J. R. & Dawkins, R.** 1984. Animal signals: mind-reading and manipulation. In: *Behavioural Ecology: an Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 380–402. Oxford: Blackwell Scientific.
- Loher, W.** 1989. Temporal organization of reproductive behavior. In: *Cricket Behavior and Neurobiology* (Ed. by F. Huber, T. E. Moore & W. Loher), pp. 83–113. Ithaca, New York: Cornell University Press.
- Loher, W. & Rence, B.** 1978. The mating behaviour of *Teleogryllus commodus* (Walker) and its central and peripheral control. *Zeitschrift für Tierpsychologie*, **46**, 225–259.
- Marden, J. H. & Waage, J. K.** 1990. Escalated damselfly territorial contests are energetic wars of attrition. *Animal Behaviour*, **39**, 954–959.
- Maynard Smith, J.** 1972. *On Evolution*. Edinburgh: Edinburgh University Press.
- Maynard Smith, J.** 1982. *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.
- Maynard Smith, J.** 1982. Do animals convey information about their intentions? *Journal of Theoretical Biology*, **97**, 1–5.
- Maynard Smith, J.** 1994. Must reliable signals always be costly? *Animal Behaviour*, **47**, 1115–1120.
- Maynard Smith, J. & Parker, G. A.** 1976. The logic of asymmetric contests. *Animal Behaviour*, **24**, 159–175.
- Morris, D.** 1957. 'Typical intensity' and its relation to the problem of ritualisation. *Behaviour*, **11**, 1–12.
- Moynihan, M.** 1982. Why is lying about intentions rare during some kinds of contests? *Journal of Theoretical Biology*, **97**, 7–12.
- Neat, F. C., Huntingford, F. A. & Beveridge, M. M. C.** 1998. Fighting and assessment in male cichlid fish: the effects of asymmetries in gonadal state and body size. *Animal Behaviour*, **55**, 883–891.
- Parker, G. A.** 1974. Assessment strategy and the evolution of fighting behaviour. *Journal of Theoretical Biology*, **47**, 223–243.
- Phillips, L. H. II & Konishi, M.** 1973. Control of aggression by singing in crickets. *Nature*, **241**, 64–65.
- Rence, B. & Loher, W.** 1977. Contact chemoreceptive sex recognition in the male cricket, *Teleogryllus commodus*. *Physiological Entomology*, **2**, 225–236.
- Shuvalov, V. F. & Popov, A. V.** 1973. Study of the significance of some parameters of calling signals of male crickets *Gryllus bimaculatus* for phonotaxis of females. *Journal of Evolutionary Biochemistry and Physiology*, **9**, 152–156.
- Simmons, L. W.** 1986. Inter-male competition and mating success in the field cricket, *Gryllus bimaculatus* (De Geer). *Animal Behaviour*, **34**, 567–579.
- Simmons, L. W.** 1986. Female choice in the field cricket *Gryllus bimaculatus* (De Geer). *Animal Behaviour*, **34**, 1463–1470.
- Staudacher, E. & Schildberger, K.** 1998. Gating of sensory responses of descending brain neurones during walking in crickets. *Journal of Experimental Biology*, **201**, 559–572.
- Stevenson, P. A., Hofmann, H. A., Schoch, K. & Schildberger, K.** 2000. The fight and flight responses of crickets depleted of biogenic amines. *Journal of Neurobiology*, **43**, 107–120.
- Tinbergen, K.** 1953. Fighting and threat in animals. *New Biology*, **14**, 9–24.
- Tregenza, T. & Wedell, N.** 1997. Definitive evidence for cuticular pheromones in a cricket. *Animal Behaviour*, **54**, 979–984.
- Turner, G. F. & Huntingford, F. A.** 1986. A problem for game theory analysis: assessment and intention in male mouthbreeder contests. *Animal Behaviour*, **34**, 961–970.
- van Rhijn, J. G.** 1980. Communication by agonistic displays: a discussion. *Behaviour*, **74**, 286–293.
- Wagner, W. E., Jr.** 1989. Fighting, assessment, and frequency alteration in Blanchard's cricket frog. *Behavioral Ecology and Sociobiology*, **25**, 429–436.
- Zahavi, A.** 1975. Mate selection—a selection for a handicap. *Journal of Theoretical Biology*, **53**, 205–214.