

Agonistic behaviour in male and female field crickets, *Gryllus bimaculatus*, and how behavioural context influences its expression

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(Received 13 April 1994; initial acceptance 16 April 1994;
final acceptance 23 June 1994; MS. number: A6837R)

Abstract. Previous interactions with conspecifics influenced the pattern, frequency and intensity of agonistic behaviour in the field cricket *Gryllus bimaculatus*. Tactile contact appeared to be the most important sensory cue responsible for the observed shifts in behaviour. Contact with other adult males promoted the production of aggressive song both during and after fights between males. However, individually housed males and males with restricted contact with conspecifics (once per day for 5 days) produced their aggressive song only at the end of an agonistic encounter. These two patterns of agonistic behaviour may reflect alternate fighting strategies. Prior experience influences whether sensory cues from a conspecific will initiate agonistic behaviour. After males lost a fight, they displayed no further agonistic behaviour for 10 min but then gradually recovered their agonistic behaviour within an hour. This may be an important mechanism in preventing losing males from re-engaging a more powerful rival. Females were much less likely than males to attack conspecifics when food was plentiful. When food was scarce, females fought more often, and more successfully, than males for the contested resource.

Crickets, like other animals, live in a dynamic social environment. Population density, for example, can vary considerably within a cricket's lifetime (Hissmann 1990). This may increase the adaptive value of some behaviour patterns while decreasing the value of those that had originally been the best suited. For example, as population density declines in the field cricket *Gryllus campestris*, actively searching for mates becomes a less successful mating strategy than calling for females from a stationary burrow (Hissmann 1990). In a related example, a *G. bimaculatus* male will typically attack other males that approach its burrow. However, defending males may eventually be challenged by a more powerful rival, in which case attacking an intruder may no longer be the most adaptive option. As these cases illustrate, it is to an animal's advantage to modify its behaviour in response to changes in its social environment.

Such shifts in behaviour are well known for a variety of species in both vertebrates and invertebrates (see Grier & Burk 1992). What is less well known is how these shifts take place. This is unfortunate because such information can provide insight into the proximate mechanisms involved in behavioural plasticity, and give us clues into the possible functions of the shift for the animal.

In this paper we examine how both male and female crickets change their agonistic behaviour depending on the behavioural context.

In the field, *G. bimaculatus* males occupy rock crevices or other natural shelters and defend them against other males (A. V. Popov, personal communication). From these shelters males attract females by emitting a species-specific calling song. Calling song also attracts males (Pollack 1982), however, leading to conflicts over burrow ownership. In the laboratory, females prefer to mate with males that possess burrows, resulting in a higher mating success for male crickets that successfully obtain and hold a burrow (Simmons 1986). Similarly, mating success in the field crickets *Teleogryllus oceanicus* and *Gryllus integer* is strongly correlated with success in agonistic encounters (Burk 1979; Cade 1979). Therefore modifications in agonistic behaviour may have large repercussions on a male's mating success.

The general form of agonistic behaviour in *G. bimaculatus* has been previously described and is known to vary depending on the social environment (Alexander 1961; Burk 1979; Simmons 1986). In the first section of this paper, we present a quantitative description of the behaviour and then measure how the behaviour changes

under different conditions. Although alternative forms of agonistic behaviour have not been reported for other crickets, *G. integer* males can adopt alternative sexual strategies (Cade 1979) illustrating the cricket's potential for behavioural flexibility.

Most earlier studies of cricket agonistic behaviour have focused exclusively on male crickets, to the neglect of investigating the agonistic behaviour of females (but see Fuentes & Shaw 1986 on *T. oceanicus*; von Hörman-Heck 1957 on *G. campestris*). In *G. bimaculatus*, females were reported not to engage in intense agonistic behaviour but their behaviour was not rigorously studied (von Hörman-Heck 1957). Moreover, in competition for a resource that is needed by both sexes, such as food, both males and females might be expected to vie for that resource. Thus we examined agonistic behaviour in females of *G. bimaculatus* and the contexts under which it occurs.

METHODS

Animals

Gryllus bimaculatus were obtained from our laboratory colony. Animals were maintained at 28°C on a 14:10 h light:dark cycle and at approximately 65% relative humidity. Crickets were fed cat chow and water ad libitum. During the last larval instar males and females were transferred to individual cages (8 cm high × 10 cm in diameter) unless otherwise noted. Solitary crickets were kept in individual containers, but were housed in the colony room. Although they received no tactile contact from conspecifics, individually housed crickets could potentially see, hear and smell other crickets. After the final moult, we marked animals for identification with typewriter correction fluid. We used sexually mature crickets 10–25 days after their adult moult. Even within this range, we always paired crickets with opponents that were within 2 days of the same adult age. Only intact crickets that were between 2.2 and 2.4 cm in length were used for experiments. We observed animals during a 2-h period immediately prior to scotophase, when males show high sexual activity (Simmons 1988).

For behavioural testing, we placed pairs of animals into Lucite arenas (18 × 14 × 9 cm) at least 10 min prior to the trial. An opaque barrier

separated the two animals during this time. The trial was started by removing the barrier. We videotaped each trial and routinely recorded the duration of the interaction between the two animals, the highest intensity of agonistic behaviour achieved by each animal (see below), and the 'winner' and 'loser' of the trial. Winners and losers can normally be unambiguously recognized in cricket interactions (Alexander 1961).

Behavioural Analysis (Ethogram)

To determine how behavioural context influences agonistic behaviour, we needed a baseline measure of how crickets behave. To do this we measured the transitional probabilities between discrete agonistic behavioural events for individually isolated males and females. This allowed us to assess quantitatively how the behaviour changed as the crickets interacted with conspecifics.

We placed randomly chosen pairs of males or females in a divided arena. We videotaped the interactions between 56 pairs of previously isolated, naive males and 27 pairs of naive females (crickets that had never had conspecific contact as adults prior to the trial) using an NEC colour camera fitted with a 55 mm Nikkor macrolens. Videotaped trials were viewed on an NEC high-resolution monitor. Tapes were played back using a Panasonic NV-8952 video-cassette recorder capable of a frame-by-frame display. Discrete behavioural events were identified and coded using an electronic event recorder (Eventlog from Conduit).

The division of agonistic behaviour into discrete component acts was based on our preliminary observations and on the categories derived from earlier studies of cricket agonistic behaviour (Alexander 1961; Simmons 1986), and are listed in Table I. We assigned each component of agonistic behaviour an intensity score, with behaviour that came towards the end of the interaction designated as the more intense (Table I). These behavioural categories are distinctive enough to produce a very high inter-observer reliability in the recorded sequences ($r_s=0.99$, $N=20$ different behavioural events; calculated by comparing the scores given by two different observers to behavioural sequences in six different cricket encounters; Sokal & Rohlf 1981). We determined the agonistic score of an interaction by adding up the intensity scores for each cricket.

Table 1. Aggressive types of behaviour in *G. bimaculatus* and their intensity-score value

Name	Description	Intensity score
Pause	Immobile for more than 15 s	0
Withdraw	Moves away from tactile contact	0
Antennal fencing	Crickets rapidly antennate the other's antennae	1
Rock body	Stationary cricket rocks body rapidly back and forth	1
Kick	Kicks leg towards conspecific	2
Threat posture	Raises itself on its forelegs	2
Mandible flare	Cricket hyperextends mandibles	3
Aggressive song	Stridulates aggressive song	3
Chase	Runs after conspecific	3
Bite	Pinches conspecific with mandibles	3
Lunges	Rushes conspecific with open mandibles	3
Grapple	Crickets butt heads and/or interlock mandibles and push or pull their opponent	4
Male flipped	Male flipped on its back during a grapple	No score

Because no significant trends were found in the transitional probabilities between patterns of agonistic behaviour or in the duration of the fight in males or females over the 5 days of consecutive trials, we used the median score to characterize each animal ($P > 0.1$, non-parametric analysis of behavioural frequencies and durations for related samples; Meddis 1984). We analysed behavioural transitions using a first-order Markov analysis following the procedures of Fagen & Young (1978) and Agresti (1990). In our analysis, all combinations of behaviour were possible, including the same behaviour following itself. Only types of behaviour that occurred in at least 15% of the trials at any given stage were included in the statistical analysis. This resulted in a 13×13 matrix for males, and a 10×10 matrix for females.

Sensory Cues Important for Eliciting Agonistic Behaviour

To test whether visual and/or olfactory cues are sufficient to induce agonistic behaviour in the absence of any behavioural cues from a conspecific, we placed test males ($N = 30$) in a Lucite arena and paired them with (1) dead males (frozen the previous day but presented only after they had thawed to ambient temperature) that supplied visual cues, but no behavioural cues, (2) plastic coated (Krylon clear acrylic spray) dead males that provided visual cues but no behavioural or olfactory cues, or (3) nitrogen anaesthetized (e.g. immobile) males that supplied visual and olfactory cues but no behavioural cues. Similar

experiments were performed using females as the test animals. Trials were 10 min in duration and the behaviour of the test crickets were recorded.

To test the effectiveness of visual cues alone in eliciting agonistic behaviour, we placed a mirror behind an opaque barrier, which provided a visual image to the test cricket. As in previous trials the barrier was removed and the behaviour of the cricket was recorded.

Immediately following a trial, we removed the target stimulus (the mirror, or the dead or anaesthetized cricket) and placed a live male in the arena. Only test males that displayed agonistic behaviour to the live male were included in the analysis. This eliminated those males that did not respond to the test 'crickets' because they had a low tendency to attack.

Effect of Interactions with Conspecifics on Agonistic Behaviour

We investigated whether prior interactions with conspecifics have specific effects on the form of agonistic behaviour, in addition to the decrease in intensity found by Alexander (1961) and Simmons (1986). We placed four groups of five males each in Lucite containers ($25 \times 25 \times 9$ cm) until they were 12 days past their imaginal moult. Every male had experienced at least one agonistic encounter (e.g. had exhibited mandible flare) while living with the group. We then isolated these males by placing them in individual cages for 6 h (to guarantee that there would be no residual behavioural effects of previous fights; see below),

after which we randomly paired them with other similarly treated males for agonistic behavioural trials. We videotaped the trials for a detailed behavioural analysis. We constructed an ethogram from these data as previously described. Following these trials we individually housed the males for an additional 5 days after which we re-tested their agonistic behaviour.

To determine whether the effects of social isolation were reversible we placed 20 12-day-old males that had been individually housed after their imaginal moult in group cages (five crickets/cage) for 5 days. At the end of this period we individually isolated each male for 6 h and randomly paired each for agonistic trials. Trials were videotaped for a behavioural analysis.

Effects of Performing Agonistic Behaviour

To determine the effect of winning or losing a fight on subsequent agonistic encounters, we removed either the winner or loser after the trial, and replaced it with another cricket that had not fought that day. This new trial was begun 1 min, 5 min, 10 min, 20 min, 1 h or 1 day after the initial agonistic encounter had ended. We recorded the behaviour of the two crickets and the trial outcome. Only crickets that exhibited grappling behaviour during the initial agonistic encounter were used in this experiment. We tested 10 winners and 10 losers at each of the six inter-encounter time intervals (e.g. a total of 60 winners and 60 losers were tested; individuals were used only once).

In a second series of trials, we presented males with sexually receptive females ($N=32$), instead of males, 1 or 10 min after an agonistic encounter. We recorded the behaviour of the male. As a control, we also presented males that had not fought that day with females ($N=15$).

In a third series of trials, we presented winning males with either anaesthetized males ($N=10$) or females ($N=10$) 1 min after their agonistic encounter to test whether winners required fewer cues to elicit agonistic behaviour.

Comparison of the Agonistic Behaviour of Males and Females Competing for Food

We placed three males and three females of approximately the same weight (± 0.1 g) and pronotal width (± 1 mm) in an arena ($25 \times 25 \times 9$ cm) and provided them with water,

but no food, for 5 days. Crickets were not debilitated by this treatment, and they can withstand more than 1 week without food without any increase in mortality (personal observations). We recorded the interactions between the animals 15 min after introducing food (one-fifth of a piece of cat chow) into the arena. We repeated the trial five times with five different sets of crickets.

RESULTS

Male Agonistic Behaviour

The ethogram for male agonistic behaviour is given in Fig. 1a. In brief, after a male had made antennal contact with another male, the recipient male turned, if necessary, to face its opponent and made antennal contact (34 of 44 sequences). This often led to intense bouts of antennal fencing (Fig. 1a). Whether antennal fencing occurred, the combatants either withdrew, or raised themselves on their forelegs (threat posture). This was typically followed by both animals hyperextending their mandibles (mandible flare). During this display, the crickets would often butt one another with their heads. In 24 of 42 cases this led to an interlocking of mandibles. The crickets would then push and pull their opponents. This sequence typically ended with one of the crickets being flipped onto its back. This animal then scurried away from its opponent, which usually chased after it, mandibles spread, stridulating the aggressive song. This song is easily distinguished from the two other songs that the cricket produces: courtship song, which is much softer, and calling song, which has a different temporal pattern.

The intensity of agonistic behaviour varied between animals within a pair as well as between pairs. Some fights ended before the high intensity behaviour of grappling or mandible flare occurred. In all cases, the fights were terminated when one of the two males withdrew from the other. We never observed any serious injury to either combatant, such as a loss of appendages, under these circumstances.

Of the 88 agonistic encounters analysed, the median agonistic score was 6 (4 and 8 being the first and third quartiles). The average (\pm SD) duration of a fight (measured from antennal contact to the withdrawal of the loser) was 5.5 ± 2.7 s (range=3–15 s). The winning male produced

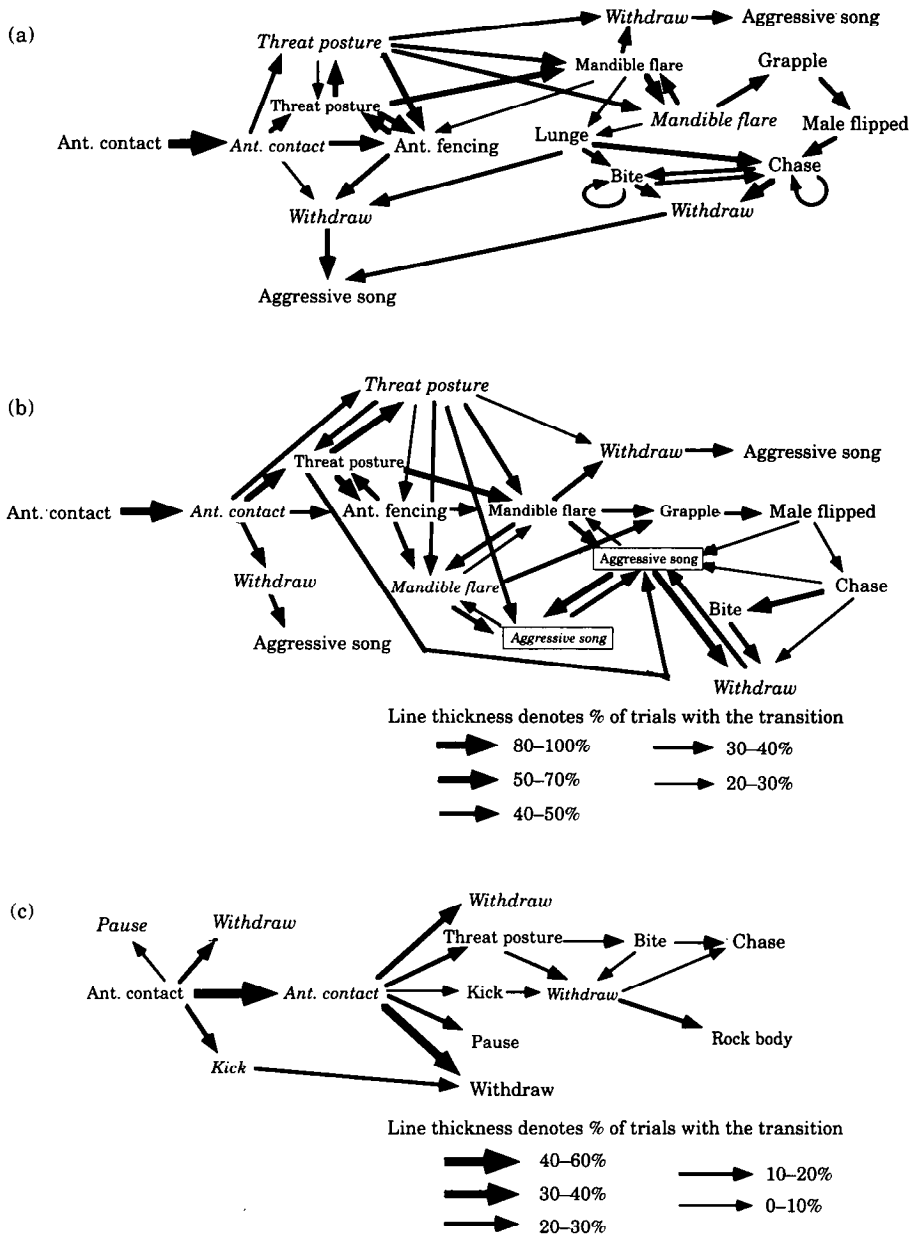


Figure 1. (a) Ethogram of the agonistic behaviour of male *G. bimaculatus* that had been isolated as adults. Only statistically significant transitions are shown. The behavioural patterns used in the figure are described in Table I. Note that only the winning male sings aggressive song, and that this song is produced only at the end of the interaction when the outcome has already been determined. Roman text represents the actions of the male that eventually prevails, while italic text represents the actions of the male that ultimately loses. (b) Ethogram of the agonistic behaviour of male *G. bimaculatus* that had been reared in a group environment. Only statistically significant transitions are shown. Note that both winning and losing males produce aggressive song (boxed text). Aggressive song occurs both at the end of the behavioural sequence as well as during the fight before the outcome has been determined. (c) Ethogram of the agonistic behaviour of female *G. bimaculatus*. Ant. fencing: Antennal fencing; Ant. contact: antennal contact.

Table II. Male and female responses to anaesthetized conspecifics

Sex of cricket tested	N	No. exhibiting agonistic behaviour			No. exhibiting courtship behaviour		
		Anaesthetized	Control*	P	Anaesthetized	Control*	P
Response to anaesthetized females							
Male	30	3	0	NS	12	28	<0.05
Female	30	1	5	NS	0	0	NS
Response to anaesthetized males							
Male	30	5	26	<0.05	0	2	NS
Female	30	0	3	NS	0	0	NS

*Control animals were active conspecifics.

aggressive song for 3.1 ± 1.3 s after his encounter. However, the pattern of the behaviour was highly variable.

The probability of an attack (grappling or lunging) was dependent on the behaviour of the conspecific. Males that withdrew from the initial antennal contact were significantly less likely to be attacked. If a male withdrew or paused in response to antennal contact, it was bitten, chased or lunged at only three of 15 times, while males that responded to antennal contact with threat posture or antennal fencing were attacked in 32 of 38 incidences (G -test: $P < 0.01$). Thus, attacks were significantly more likely against any animal, male or female (see below) that engaged in antennal fencing or threat posture.

Female Agonistic Behaviour

An ethogram for female agonistic behaviour is shown in Fig. 1c. Females were significantly less likely to attack a same-sex conspecific than were males (female median agonistic score was 0; 0 and 1 for the first and third quartiles, $N = 56$; 27 pairs, two-sample test for frequency: $z = 2.85$, $P < 0.05$; Meddis 1984). The fights were also shorter, with a mean duration of 2.2 ± 1.3 s (t -test: $P < 0.05$).

In one of the 27 female–female pairs, one female lifted its wings slightly and rapidly vibrated them. The display was very short and looked as if it were analogous to aggressive singing in males, although the movement produced no audible sounds. (Female *G. bimaculatus* lack the necessary wing specializations to produce sound.)

Female *G. bimaculatus* will occasionally interlock mandibles (personal observations), although this behaviour is rare and was not seen in the 27 videotaped pairs of females.

Sensory Cues Important for Eliciting Agonistic Behaviour

Neither males ($N = 30$) nor females ($N = 30$) attacked their own reflections in the mirror nor did they attack dead or plastic coated conspecifics. Females rarely attacked anaesthetized conspecifics (Table II). Males, however, attacked anaesthetized males, but significantly less often than they did active males (Table II). They attacked anaesthetized males by biting them with their mandibles, but often without first exhibiting mandible flare. In three cases the male uttered a burst of aggressive song after extensive maxillary palp and antennal contact with the anaesthetized male. Only one male ($N = 30$) produced aggressive song after contacting an anaesthetized female.

Effect of Interactions with Conspecifics on Agonistic Behaviour

Figure 1b depicts the ethogram for aggression among males that experienced contact with conspecifics during their period of sexual maturation (mature male sexual behaviour is fully developed 1 week after their last moult; personal observations).

Although there was no significant change in the mean duration of the fight (5.2 ± 4.2 s; t -test: $N = 10$, $P > 0.1$) there was a notable change in the time of occurrence of aggressive song (Fig. 1) and in its frequency compared with individually housed crickets (Fig. 2). In crickets that had been kept in groups of five for a week, both winning and losing males stridulated during the middle phase of the fight. Among the males that had been individually housed for a week after the adult moult, only the winning male stridulated,

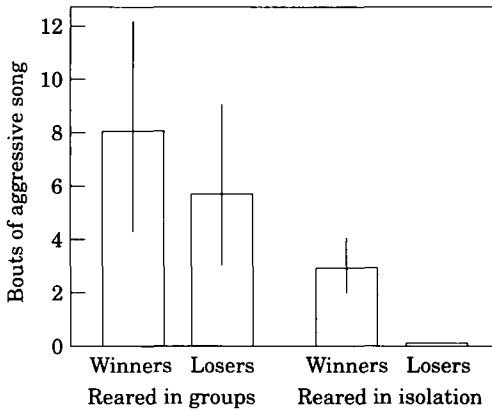


Figure 2. Isolated male crickets produced less aggressive song than those reared in groups. Histogram bars represent the median number of bouts of aggressive song produced during the interaction (including the aggressive singing of the winner at the end of the interaction). The error bars represent the first and third quartile values. Winners sang more than losers ($N=10$, $P<0.05$), and crickets reared in groups sang more than crickets reared in isolation ($N=10$, $P<0.05$, non-parametric planned comparison; Meddis 1984).

and then he usually did so only after the other male had fled (Fig. 1). This pattern of aggressive singing in individually housed crickets persisted even when these crickets were subjected to daily trials of conspecific contact for 5 consecutive days.

However, this behaviour could be altered by extended tactile and/or olfactory contact with other crickets. If individually housed males were then grouped together in an arena for 5 days, they developed the group pattern of aggressive singing (Fig. 3). Similarly, males from the group cages that were individually housed for 5 days began to exhibit the pattern of aggressive singing seen in isolated crickets (Fig. 3).

Agonistic Encounters Affect Subsequent Behaviour

Males that lost a high-intensity agonistic encounter (one that contained a grappling sequence), showed a complete suppression of all agonistic behaviour for at least 10 min (Fig. 4). After losing a fight, losing males no longer responded to conspecific antennal contact from another male with threat postures and antennal fencing, but instead fled from other males. However, 1 h later, losing males responded to

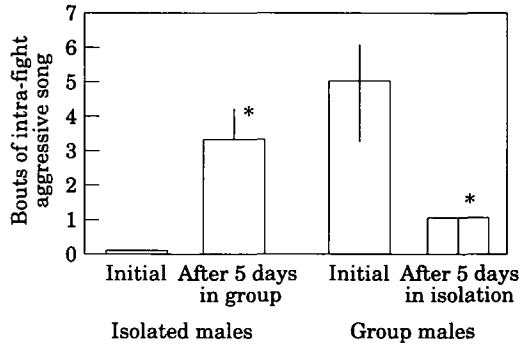


Figure 3. The pattern of aggressive singing in males ($N=20$) following interactions with other males. Histogram bars represent the median number of aggressive singing bouts that occurred before the end of each interaction. The error bars represent the first and third quartile values. *Initial values that differed significantly from the final value ($P<0.01$) as determined by a Wilcoxon test.

conspecific antennal contact with typical agonistic behaviour.

Winning males also showed short-term behavioural changes. Immediately after winning a fight, they attacked males with a shorter latency (0.9 ± 0.3 min versus 0.4 ± 0.3 min after; Wilcoxon test: $N=19$, $P<0.05$), and their opponent was defeated in 18 of 19 trials. These effects were measurable for up to 10 min after the initial fight. It is notable that winning males did

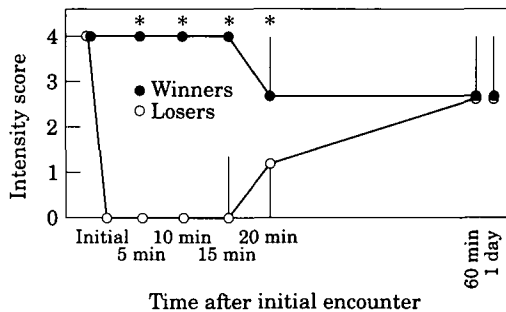


Figure 4. Effects of interactions with conspecifics on agonistic behaviour. Most of the data points have no error bars because all crickets in the sample ($N=10$ for each time point for both winners and losers) scored the same value. Where this was not the case, error bars denote the first and third quartile value. In some cases, the quartile value was the same as the median, therefore only one error bar is visible. *Values that differed significantly between winners and losers ($P<0.01$, non-parametric planned comparison; Meddis 1984).

Table III. Mean number of occurrences per cricket per sequence of different components of agonistic behaviour under different behavioural contexts

Behaviour	Male		Female	
	Inter-male conflict (<i>N</i> =56)	Conflict for food (<i>N</i> =20)	Inter-female conflict (<i>N</i> =27)	Conflict for food (<i>N</i> =20)
Antennal fencing	1.1 ± 0.2	0.8 ± 0.3	0.8 ± 0.4	0.7 ± 0.4
Kick	0.04 ± 0.06	0.6 ± 0.2*	0.2 ± 0.2	0.7 ± 0.3*
Threat posture	0.8 ± 0.4	0.6 ± 0.4	0.3 ± 0.2	0.6 ± 0.2
Aggressive song	5.3 ± 3.2	1.2 ± 0.8*	0	0
Bite	1.2 ± 1.3	3.2 ± 0.6*	0.2 ± 0.4	4.3 ± 1.5*
Lunges	0.3 ± 0.3	1.4 ± 0.8	0 ± 0.1	1.4 ± 1.6*
Grapple	0.7 ± 0.3	0.04 ± 0.01*	0	0

*Behaviour within each sex that differed between intra-sexual conflicts and conflicts over food (repeated-measures two-way ANOVA: $P < 0.05$).

not attack anaesthetized females, although they bit and stridulated aggressive song towards eight of 10 anaesthetized males.

Performing agonistic behaviour affected subsequent courtship as well. Winning males were more likely to attack rather than court a sexually receptive female 1 min after an agonistic encounter than they were before an agonistic encounter (1 of 16 before; 5 of 16; McNemar test: $P < 0.1$). Similarly, control males that had been paired with nymphs instead of other males, and therefore had not fought immediately prior to contacting the female, attacked females less than did winning males (1 of 15; *G*-test: $P < 0.1$). However, once courtship had been initiated, there was no significant effect of prior winning or losing a fight on the duration of courtship (winners: 55 ± 4.3 s; losers: 60 ± 5.6 s, $N=16$) or on the likelihood that courtship would lead to successful copulation (winners: 15 of 16 successful; losers: 16 of 16 successful; *G*-test: $P > 0.1$).

Comparison of the Agonistic Behaviour of Males and Females when Competing for Food

When weight-matched, food-deprived male and female crickets were placed together with limited amounts of food, females won $68.6 \pm 18\%$ of fights against male crickets ($N=44$ fights recorded from the five different groups of crickets). Females were in contact with the food for 9.3 ± 3.8 min over the five trials, while males were in contact with the food for 4.2 ± 2.7 min, which was significantly less than the females (*t*-test: $P < 0.05$). Females fought more fights during the 15-min

trial against both females and males for access to food than did males (females fought 17.4 ± 5.2 fights in 15 min, males fought an average of 10.8 ± 6.2 fights; *t*-test: $P < 0.10$). During agonistic encounters under these conditions, males produced aggressive song in 12 of 44 observed male–female encounters. In only five of these encounters did the male wrest the food from the female.

Both males and females displayed threat postures to each other, and females were as likely to bite or lunge as were males (females initiated bites or lunges in 20 of 44 fights observed between male and female crickets, while males initiated bites or lunges in 16 of the encounters).

The frequencies of some patterns of agonistic behaviour differed during fights for food from those frequencies observed during the inter-male and inter-female agonistic encounters. Kicking, lunging and biting were more frequent for both sexes. Grappling was less frequent in males, although it did occur (Table III).

DISCUSSION

The pattern of agonistic behaviour in *G. bimaculatus* can have more than one form. For example, both male and female *G. bimaculatus* changed their pattern of agonistic behaviour depending on whether they were fighting over a food pellet or were engaged in a hierarchical conflict (Table III). When fighting for food, crickets grappled less with each other, and relied more heavily on behaviour such as kicking and biting, which allowed them to repel competitors and still remain close to the contested resource.

Sharing a living area with conspecifics resulted in an agonistic behavioural pattern in which the winning male sang aggressive song in the middle of a fight. Individually housed males, however, produced aggressive song only at the end of the fight, after the outcome had been determined. Understanding why crickets living in groups differed from individually housed crickets in the timing of their aggressive song requires an understanding of the function of aggressive singing in cricket agonistic encounters. Although it has been suggested that aggressive singing inhibits an opponent's tendency to attack (Phillips & Konishi 1973: *Acheta domesticus* and *Gryllus pennsylvanicus*; Alexander 1961: North American *Gryllus* species), mute males are as successful at winning fights as controls (*G. bimaculatus*: S. A. Adamo & K. Schilberger, personal observations; *A. domesticus*: T. G. Nolen, personal communication).

Burk (1979) instead suggested that aggressive songs may function as advertisement displays to other crickets. For example, these songs may decrease the tendency of nearby males to challenge a burrow owner. Given that sound production can also attract predators (Sakaluk & Bellwood 1984), crickets that have fewer conspecifics to repel may perform less singing than those in more crowded environments. Males in the field do produce less aggressive song when population densities are low in a related cricket, *G. campestris* (Hissmann 1990).

Lack of conspecific contact has been shown to affect agonistic behaviour in a wide range of animals (i.e. birds and mammals; see Archer 1988), but these changes have not been examined for any possible adaptive function. Given the possible adaptiveness of these changes in *G. bimaculatus*, it seems reasonable to re-examine some of the changes seen in other animals for possible adaptive significance, especially in animals that experience large changes in population density over the course of their life span.

Agonistic behaviour in *G. bimaculatus* usually requires information from more than one sensory modality before it is initiated. Visual cues alone never elicited agonistic behaviour. Neither male nor female crickets attacked a mirror. (It should be noted that *G. bimaculatus* is capable of form vision; see Honneger & Campan 1989.) *Gryllus bimaculatus* does not rely entirely on chemosensory cues either and although Otte & Cade (1976) showed that males of a North American *Gryllus*

species are sensitive to the odours of conspecific females, Rence & Loher (1977) and Hardy & Shaw (1983) both showed that volatile pheromones are insufficient to induce courtship or aggressive behaviour. Male crickets attacked both male and female conspecifics that adopted a threatening posture, even after antennal contact. This suggests that behavioural cues from the opponent (and these are likely to be a complex mix of visual, olfactory and tactile cues) are the most important factors in initiating and maintaining agonistic behaviour. This differs from the situation found in other crickets such as *T. commodus* in which males show intense agonistic behaviour after contact with male antennae, even if the antennae have been detached from the cricket (Rence & Loher 1977).

The intensity of sensory experience needed to elicit agonistic behaviour depends on previous experience. For example, only males that had recently won an agonistic encounter tended to attack anaesthetized conspecifics. Usually male and female crickets require behavioural cues before initiating an attack.

Tactile contact and/or olfactory cues appear to determine the type of agonistic behaviour that a cricket adopts. Merely hearing conspecifics (the individually housed males were kept in a room filled with singing crickets) is not sufficient to bring about the group pattern of agonistic behaviour, nor is a single agonistic encounter once a day for 5 days, suggesting that repeated tactile and/or olfactory contact is necessary. In other species of crickets, tactile contact has been shown to influence the prevalence of macropterous (long-winged) and micropterous (short-winged) variations (Masaki & Walker 1987) demonstrating that this sensory input can have a strong influence on a cricket's physiology.

After being defeated, males suppress their agonistic behaviour for up to 10 min. The inhibition of agonistic behaviour may be adaptive in that it prevents the cricket from continuing to fight a more powerful opponent, thus avoiding injury. This mechanism may be important in field crickets, which appear not to use individual recognition to identify more powerful males (Burk 1979). The losing cricket's agonistic behaviour does not return until it has had time to move away from the more powerful cricket's burrow area.

Crickets differ from mice (Leshner 1980), swordtail fish (Hannes et al. 1984) and other

species (see Archer 1988) in which the outcome of a fight has a long-term (days as opposed to minutes) effect on a participant's behaviour. In many of these other species, however, the animals are capable of individual recognition (Brown & Colgan 1986; Hurst et al. 1993), therefore long-term changes in agonistic behaviour can be sculpted specifically for different conspecifics.

Although *G. bimaculatus* females were less likely to attack conspecifics when resources were plentiful, when food resources were scarce, they fought more than males did. Males, despite their larger agonistic behavioural repertoire, were not more successful at competing for a scarce resource than were females. Even as nymphs, females are more successful than males at sequestering food (Simmons 1987). Therefore, although the males' agonistic behaviour is more conspicuous, and certainly noisier, this does not necessarily mean that males are more 'aggressive' under all conditions. This will vary depending on the context of the interaction, and cannot be predicted from the intensity of inter-male contact, or from the complexity of inter-male displays.

In many insects, egg production requires more energy than does sperm production (Thornhill & Alcock 1983). This is likely to be true in crickets as well, given the capacity of females to produce many hundreds of eggs during their lifetime. The females used in the food deprivation experiment were not virgins and therefore the food may have been a more 'valuable' resource to them (i.e. for egg production) than it was to the males. This may partly explain why the females were more aggressive than the males under conditions of food deprivation.

ACKNOWLEDGMENTS

We thank Derek Ochiai for his assistance in data collection and Paul Faure and Bob Wyttenbach for their comments on the manuscript. This work was supported by a Natural Sciences and Engineering Research Council of Canada Post-doctoral Fellowship to S.A.A. and by a Javits/Pepper Neuroscience Award from the NIDCD, NS11630 to R.R.H.

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