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Information asymmetry and aggressive behaviour in male house crickets, *Acheta domesticus*

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Aggressive interactions can play an important role in the reproduction of many species. Several factors (e.g. resource value, asymmetries among contestants in fighting ability, and information asymmetry) influence the amount of aggression shown by individuals. In particular, it has been predicted that resident individuals, who presumably have more information about an area than nonresidents, will be more likely to win when the area contains resources of high value. Conversely, invaders, who have incomplete information about an area, should be more likely to win when the resource value is low. Male house crickets, *Acheta domesticus*, increase their aggressive behaviour in the presence of female chemical cues; thus, we manipulated the amount of chemical cues in a given area and who had information (resident versus invader). Resident males were more aggressive and won more contests when there was a greater amount of female chemical cues. In addition, invader males were more likely to win contests under control conditions with no female cues. Our data suggest that information asymmetry can play an important role in the fighting decisions made by animals. Additionally, our data highlight the multimodal nature of communication in crickets.

Keywords: *Acheta domesticus*; aggressive behaviour; Gryllidae; house cricket; resident–intruder asymmetry

Aggressive interactions play a critical role in the reproductive success in many taxa (Tachon et al. 1999; Berglund & Rosenqvist 2000; López et al. 2002; Double & Cockburn 2003; Rantala & Kortet 2004; Savage et al. 2005). These interactions are usually metabolically expensive (e.g. Hack 1997a, b; Rovero et al. 2000) and individuals can risk injury and increase their risk of predation (Huntingford & Turner 1987). Contests may be mediated by asymmetries in information, resource-holding potential (RHP), motivation, and ownership (Bridge et al. 2000; López & Martín 2001; Kemp 2003; Kemp & Wicklund 2004; Brown et al. 2006). Resource value has a key role in influencing an individual's aggressive behaviour (Austad 1983; Enquist & Leimar 1987; Otto 1989; Gray et al. 2002; Nosil 2002; Gherardi 2006; Humphries et al. 2006) and territory holders (or resident individuals), who should have more information about an area than intruders, should show higher levels of aggression towards intruders or increased willingness to fight when a resource is worth more (Austad 1983; Otto 1989; Riechert 1998; Bridge et al. 2000; Stocker & Huber 2001; Guerra & Mason 2005). For example, male orb-weaving spiders, *Metellina mengei*, are more likely to escalate aggressive interactions when they are defending larger and more fecund females (Bridge et al. 2000).

Enquist & Leimar (1987) predicted: (1) when individuals invading a territory have imperfect or incomplete information about the value of a territory, they might be victorious when the resource is not highly valued; (2) that the owner's probability of winning the contest will be greater when the value of the resource is greater; (3) that the costs of contests would rise for both individuals as the value of the resource increased; (4) that as resources increased, residents would be more likely to escalate rapidly compared to invaders. Male field crickets frequently show displays of aggression towards each other (Alexander 1961) and are willing to fight over various types of resources (e.g. food: Nosil 2002; mates: Tachon et al. 1999). These displays consist of a series of stereotypical behaviours (Alexander 1961; Hofmann & Schildberger 2001) that escalate from energetically inexpensive behaviours

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(e.g. antennation/antennal fencing and stridulation) to more expensive and higher risk behaviours, such as mandible flaring and grappling (Hack 1997b). Fighting success in crickets is a function of RHP, which is partially determined by body size (e.g. Dixon & Cade 1986), burrow residency (e.g. Simmons 1986; Hack 1997a), and prior fighting success (e.g. Savage et al. 2005). In most cricket species, larger males tend to win contests, although not always, and these contests are energetically expensive (Hack 1997a, b). In the house cricket, *Acheta domesticus*, burrow residency, body size, and prior fight outcomes influence the likelihood of a male winning a contest, and male attractiveness is correlated with fighting ability (Hack 1997a; Savage et al. 2005; Brown et al. 2006).

We tested two of the predictions of the model of Enquist & Leimar (1987) by manipulating the information available to male house crickets via chemical cues. Male house crickets increase the amount of aggressive behaviour in the presence of chemical cues from females (Otte & Cade 1976). Thus, we can manipulate (1) perceived resource value via chemical cues and (2) the amount of information an individual has about the resource by manipulating the time available for a male to explore the territory. We predicted that (1) residents will be more aggressive than intruders and win more contests when the value of the resource is high and (2) invaders will be more aggressive and more likely to win encounters when the resource value is low.

METHODS

Acheta domesticus were reared from laboratory stock in 84-litre plastic containers with a 14:10 h light:dark cycle at 25°C and constant humidity. Egg cartons were provided as habitat structure and moistened vermiculite was available for oviposition. Cotton-plugged water vials and cat food (Purina Cat Chow) were supplied ad libitum in each container. The stock population was originally purchased from Reeves Cricket Ranch where they maintain a population of 4–6 million individuals with 250 000 adult breeders. Over the last 10 years, this population has been supplemented with individuals from other populations of several different cricket breeders (C. Reeves, personal communication). Male and female virgin crickets were isolated immediately after the development of their wings. Each cricket was placed in a container (15 × 15 × 5 cm) with cat food and water available ad libitum. Males and females were housed individually for at least 1 week but no more than 2.5 weeks. Crickets younger than 1 week and older than 6 weeks are significantly less aggressive (Hofmann & Schildberger 2001). Thus, only crickets between 7 and 19 days of adult age were used in this study.

All fights were staged in containers (14 × 26 × 11.5 cm) filled with about 2–3 cm of sand. Preparation of female chemical cues and males for fights occurred 48 h prior to trials. Treatments consisted of one female ($N = 24$), two females ($N = 28$), or three females ($N = 26$) placed in the containers for 48 h. After 48 h, all females, if any, were removed from the containers. Our treatment assumes that by varying the number of females in the container, we have manipulated the amount of female cues (e.g. pheromones or faeces). Controls were prepared like the female cue treatments but with no females placed in the containers ($N = 26$).

Forty-eight hours prior to trials, males were weighted to the nearest tenth of a milligram using an Ohaus adventurer analytical balance and were marked individually on the tibia using a small dot of Testor's Model paint. Males were then randomly assigned as either the resident or invader. The resident male was placed in the test container for 1 h prior to the start of the trial to gain information about the container. The invader male was then introduced and both crickets were isolated in individual vials in the container for about 5 s. Vials were lifted to start the trial and interactions between the crickets were observed and videotaped for 10 min with a Sony DCR-TRV33 mini-dv recorder.

Crickets show a number of behaviours during aggressive interactions, and as fights escalate, they show different behaviours. This stereotypical sequence of behaviours can be used to determine the outcome of fights (e.g. Alexander 1961; Savage et al. 2005; Brown et al. 2006). Lower levels of escalation are indicated by antennal fencing/antennation and are followed by a series of more dramatic and energetically expensive behaviours (e.g. mandible flares and grappling, Hack 1997b).

We analysed each video using JWatcher (http://www.jwatcher.ucla.edu), a java-based behavioural analysis program. We recorded whether or not each individual showed aggression, the frequency of encounters, antennation and stridulation (aggressive singing) for residents and invaders over the 10-min observation period. Since each trial had multiple encounters between resident and invader males, males were considered winners of contests if they showed clear dominance over the other male (e.g. the other male always retreats) and if this was not clear, the winner was assigned based on which male retreated more often (Brown et al. 2006).

Whether an individual showed aggression or not was modelled using a repeated measures approach to modelling categorical data. Briefly, we used a generalized estimating equation (GEE) approach (Liang & Zeger 1986). GEEs allowed us to use a generalized linear model and account for the potential correlation between resident and invader behaviour in the same trial. In addition, this approach allowed us to test our predictions about these data using a single model rather than fitting two logistic regressions, one for residents and one for intruders. We fitted a generalized linear model with GEE in PROC GENMOD in SAS v. 9.0 (Liang & Zegler 1986; Stokes et al. 1995; SAS Institute Inc. 2004). Because the response variable is binary (aggressive behaviour was observed or it was not), we assumed a binomial distribution and a logit link and fitted a model that included two factors (residency status and number of females used to lay down cues) and their interaction. We assumed an unstructured correlation structure when constructing this model (Liang & Zegler 1986; Agresti 2002). However, the choice of correlation structure did not change the outcome of our analysis. We predicted that there would be an interaction between residency status and the amount of chemical