

A behavioural syndrome in the field cricket *Gryllus integer*: intrasexual aggression is correlated with activity in a novel environment

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Behavioural syndromes, or suites of correlated behaviours across different contexts and situations, have recently drawn attention from evolutionary biologists. In the field cricket *Gryllus integer*, males are aggressive with one another and fight vigorously over females and territories. We examined whether aggressiveness with other males was correlated with activity in a potentially dangerous context (a novel environment) in laboratory-raised virgin males. Aggressiveness was measured as fighting ability against a weight-matched opponent. First, we measured each cricket's latency to become active in a novel environment and latency to emerge from a refuge within a novel environment. Next, we determined which of two weight-matched males was more aggressive, by pitting the males together in an agonistic contest and counting the number of fights won by each male. More aggressive males, who won more fights, had shorter latencies to become active when placed in a novel environment and shorter latencies to emerge from a safe refuge. These results suggest that a behavioural syndrome exists in *G. integer*, in which more aggressive males are also more active in general, and possibly less cautious towards predation risk. © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, 91, 475–482.

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INTRODUCTION

Recent studies support the existence of behavioural syndromes, comprising suites of correlated behaviours across different situations or contexts (Hedrick, 2000; Gosling, 2001; Sih, Kats & Maurer, 2003; Sih *et al.*, 2004b; Sih, Bell & Johnson, 2004a; Carere & Eens, 2005). One of the most familiar behavioural syndromes in animals is an aggressiveness/activity syndrome, in which individuals behave more or less aggressively/are more or less active across many contexts (Sih *et al.*, 2004a,b). For example, in funnel-web spiders, some individuals are more aggressive with conspecifics than others, attack prey more vigorously, and expose themselves to higher risk of predation

because of their 'bold' or incautious behaviour in the presence of predators (Hedrick & Riechert, 1989, 1990; Riechert & Hedrick, 1993). Aggressiveness towards conspecifics that is correlated with dangerously bold or noncautious behaviour under predation risk has been demonstrated in a number of species, including stickleback fish (Huntingford, 1976, 1982; Bell, 2005) and fishing spiders (Johnson & Sih, 2005). The existence of behavioural syndromes may offer an explanation for apparently 'non-adaptive' behaviour, such as sexual cannibalism, high levels of activity under predation risk, and hyper-aggressiveness that decreases mating success by startling or driving away potential mates (Sih *et al.*, 2004a; Bell, 2005; Sih & Watters, 2005). Moreover, the persistence of behavioural 'types' within a species (e.g. 'bold' and 'shy' individuals) suggests that there can be more than one

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general adaptive strategy for individuals within that species (Dall, 2004). For example, aggressive individuals that are incautious in terms of predation risk and less aggressive individuals that are cautious in terms of predation risk may have similar fitnesses (Riechert & Hedrick, 1993; Dall, Houston & McNamara, 2004; Dingemans *et al.*, 2004).

In species with social dominance hierarchies, such as field crickets (*Gryllus* spp.), more aggressive males achieve higher dominance status by winning fights (Alexander, 1961; Andersson, 1994; Berglund, Bisazza & Pilastro, 1996; Rantala & Kortet, 2004). Males fight for and defend territorial shelters and females (Alexander, 1961; Simmons, 1986a; Adamo & Hoy, 1995; Hofmann & Schildberger, 2001; Kortet & Hedrick, 2005; Väänänen, Kortet & Rantala, 2006), and success in intrasexual competition can result in increased fertilization success for dominant males (Simmons, 1986b; Rantala & Kortet, 2004; Kortet & Hedrick, 2005). Fighting success is a heritable trait in at least one species of field cricket (*Gryllus bimaculatus* De Geer; Wedell & Tregenza, 1999).

Virtually no studies have investigated behavioural syndromes in field crickets (but see Hedrick, 2000) even though many behavioural traits, such as mating preferences, antipredator behaviour, aggression, and social dominance have been studied in these animals (Adamo & Hoy, 1995; Hedrick & Weber, 1998; Gray & Cade, 1999; Hedrick, 2000; Wagner & Reiser, 2000; Rantala & Kortet, 2003; Kortet & Hedrick, 2004, 2005). However, in a population of the field cricket *Gryllus integer* Scudder in Davis, California, calling behaviour is phenotypically correlated with antipredator behaviour. In this population, males call to attract receptive females, males differ in their durations of uninterrupted calling, and females prefer longer calls (Hedrick, 1986). Calling duration is heritable (Hedrick, 1994). Hedrick (2000) demonstrated that males with longer calls were more cautious about predation risk than males with shorter calls: they had longer latencies to emerge from a safe refuge in a novel environment, and had longer latencies to resume calling when interrupted by a predator cue. Aggressiveness of males was not measured in this study.

In the present study, we examined whether a general aggressiveness/activity syndrome exists in *G. integer*, by testing whether 'cautiousness' about becoming active and emerging from a safe refuge in a novel environment was correlated with the fighting ability of males. If an aggressiveness/activity behavioural syndrome exists in this population of *G. integer*, we predicted that more aggressive males (those who won the majority of fights with a weight-matched opponent) would have shorter latencies to become active and to emerge from a refuge than less aggressive males.

MATERIAL AND METHODS

CRICKETS

The crickets used in this experiment were the first laboratory generation derived from wild-caught *G. integer* females (August 2003) collected from Davis, California. In this population, males call from cracks in the ground to attract sexually receptive females, and females travel above ground to find males. Males sing at the entrance of the crack with their heads outside the crack entrance, but abruptly stop calling and run further into the crack if they sense a predator approaching. Although they leave cracks to forage, they appear reluctant to leave cracks, presumably because this increases predation risk. Similar hiding behaviour occurs in many taxa and is generally recognized as an antipredator tactic (Dill & Fraser, 1997; Hugie, 2003; Jennions *et al.*, 2003; Hugie, 2004).

Wild-caught females had been inseminated in the field before capture. Laboratory crickets were maintained at 25 ± 1 °C with food available (Purina chick starter) and water *ad libitum*, under a 12 : 12 h light/dark photoperiod. Experimental crickets were removed from bulk family boxes as nymphs (approximately one quarter adult size) and reared individually (also with food and water available *ad libitum*) in waxed cardboard cups. Individuals of both sexes were physically, but not acoustically, isolated from other individuals to ensure virginity and control for experience (with the possible exception of acoustic experience). The crickets were approximately 2 weeks past the final adult moult on the first day of the experiment.

EXPERIMENTAL TRIALS ON ACTIVITY IN A NOVEL ENVIRONMENT

Experimental trials were conducted in a sound-proof, temperature controlled dark room chamber (26 ± 1 °C), consisting of a computer, desk, and red filter light (25 W red incandescent bulb, 60 cm from the arena). The red light was used to mimic nocturnal conditions. Our methods for trials to assess the 'cautiousness' of individual crickets were as described previously (Hedrick, 2000), and resembled methods that have been used extensively to measure 'fearfulness' in rodents (Boissy, 1995). At the beginning of a trial, an experimental male was placed in a clean experimental vial (a clear plastic vial that was covered with a layer of clear tape to make it opaque, 4 cm in diameter \times 65 mm in length, set upright in an experimental arena (Rubbermaid food storage container; length 17 cm \times width 17 cm \times height 10 cm). The cricket inside the vial was given 2 min to acclimate to the environment. After acclimation, experi-

ments were started: vials were carefully laid down lengthwise in the arena, and a plexiglass cover was set over the top of the arena. The trial lasted for 10 min. If a cricket had not moved within 10 min, the trial was ended. Three times were entered into the computer during the trials using the AV Bio-Statistics Professional program, version 4.5; <http://www.cc.jyu.fi/~ansvain/avbs/>). These times were recorded and classified as: 'activity', 'head', and 'body'. 'Activity' was the number of seconds from trial initiation until the cricket's first movement inside the vial. 'Head' was the number of seconds from trial initiation until the cricket's head first emerged from the vial (the head broke the plane of the vial opening). 'Body' was the number of seconds from trial initiation until the time at which the cricket's entire body exited the vial. We found that the time at which the cricket's head emerged was highly correlated with the time at which all of the body emerged (Pearson $r = 0.902$, $N = 100$, $P < 0.001$); accordingly, we report only the 'head' times as a measure of emergence. For 'activity' times, we excluded values of 2 s or less because these probably did not reflect hiding behaviour, but rather escape behaviour. To ensure that handling did not have any effect on their behaviour, crickets were weighed after the activity trials to the nearest 0.0001 g. No cricket was used in more than one trial.

During trials, the crickets often acted 'cautiously' when emerging (e.g. they moved carefully and slowly, sometimes poking their antennae out and pulling them in again several times before emerging). As in our previous studies (Hedrick, 2000; Hedrick & Kortet, 2006), males never called from within the vial, suggesting that they did not treat it as a defensible resource. Therefore, our measurement of 'latency to emerge' apparently measured variation among crickets in predator-avoidance behaviour, as opposed to other kinds of behaviour (e.g. territoriality). Moreover, the test situation was not completely artificial for the crickets because they often fly to new habitats, where they land and then search for a safe shelter (Hedrick, 2000).

INTRASEXUAL AGGRESSION TEST PROCEDURE

We matched male contestants by weight in our study, because male weight affects fighting success in other species of crickets (*G. bimaculatus* and *Acheta domestica* L.; Hofmann & Schildberger, 2001; Savage *et al.*, 2005). Fighting success was measured within 2 weeks after the activity trials. First, the size-matched males (mean \pm SE difference in fresh weight = $1.3 \pm 0.16\%$, $N = 50$ pairs) of approximately the same age (mean \pm SE difference = 2.9 ± 0.35 days) were marked on the pronotum with enamel paint to allow recognition in trials. Next, both males within a pair and one

female (to trigger males to fight) were introduced into a sand-covered plastic arena under red-light illumination (length 20 cm \times width 20 cm \times depth 20 cm; Kortet & Hedrick, 2005). Females were used because our pilot trials suggested that, in *G. integer*, at least some males needed a female present before they would become aggressive at all. Preceding the trial, crickets were placed for in the arena under separate plastic vials for 3 min to calm them. After removal of the vials, the males usually started fighting immediately. Each trial lasted for 6 min, during which time the male–male contests were observed. The room temperature was kept at 26 ± 1 °C. To control for possible fluctuations of aggressiveness in a 24-h day, we conducted the experiments between 15.00 h and 22.00 h. The within-pair dominance status of each male was determined by the number of times he won aggressive encounters (i.e. fights, defined as continuous physical contact that included wrestling or biting). This was easy to observe because, after a fight, one of the crickets retreated (i.e. moved away from the other male) and showed avoidance behaviour (i.e. withdrew whenever the other cricket approached). We regarded retreat and avoidance as signs of submission (losing a fight). We recorded the number of fights won and lost by each male during the contest. The male that won more fights was scored as the dominant male within a pair. Females were not allowed to mate; instead they were immediately separated from males using a long thin stick (length 30 cm \times diameter 6 mm) if they started mounting a male. Generally, females did not attempt to mount males until fighting had ceased, and they did not intervene in fights.

STATISTICAL ANALYSIS

We used a paired *t*-test to compare the weights of dominant and subordinate males within pairs and Pearson's product-moment correlation coefficients to measure the correlations between weight and latency to become active, and weight and latency to emerge (Zar, 1984). To analyse data on the latency to start moving inside the refuge and the latency to emerge from hiding, we used Kaplan–Meier survival analyses (Crowley & Breslow, 1984). Specifically, we used Gehan–Breslow tests of survival data to compare survival curves from dominant vs. subordinate males. The Gehan–Breslow test is a nonparametric test using a chi-square statistic to reject the null hypothesis that two or more survival curves came from the same population. It assumes that the early survival times are known more accurately than later times and weights the data accordingly (Systat Software Inc., 2004). These tests are appropriate for our data because trials were stopped after 10 min.

RESULTS

Male weight was uncorrelated with latency to become active and latency to emerge ($N = 100$, Pearson $r = -0.0981$, $P = 0.334$; $N = 100$, Pearson $r = -0.012$, $P = 0.907$, for the first activity and the emergence time, respectively).

In each 6-min aggression trial, males engaged in one to 13 fights to establish their dominance. After the first five fights, one of the males usually won most of the further aggressive interactions, indicating that he achieved dominance status within a pair. Despite the fact that we used weight-matched male pairs, dominant males were somewhat lighter than their subordinate partners (dominant mean weight, 0.3577 g; subordinate mean weight, 0.3600 g; paired t -test, $t = -2.885$, $N = 50$, d.f. = 49, $P = 0.006$).

When we compared the latency to become active for subordinate and dominant males, our survival analysis indicated that the survival curves between subordinate and dominant diverged significantly. Dominant males started moving sooner inside the vial than did subordinate males (Kaplan–Meier survival analysis, $N = 50$, Gehan–Breslow test statistic = 5.712, d.f. = 1, two-tailed $P = 0.017$; median activity time = 109 s for dominant vs. 202 s for subordinate; Fig. 1). The latency to emerge did not differ statistically significantly for dominant and subordinate males when com-

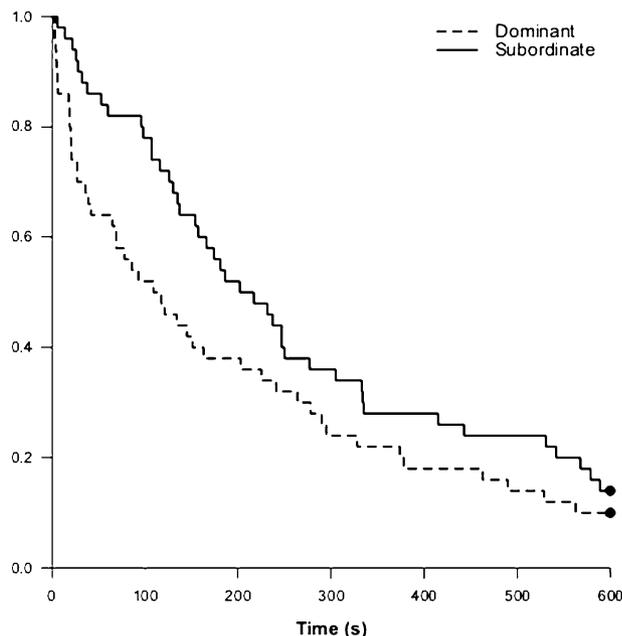


Figure 1. Proportion of crickets still immobile vs. time (s) for dominant and subordinate *Gryllus integer* males in activity trials. The male groups differed statistically significantly ($N = 100$, Gehan–Breslow test statistic = 5.712, d.f. = 1, two-tailed $P = 0.017$).

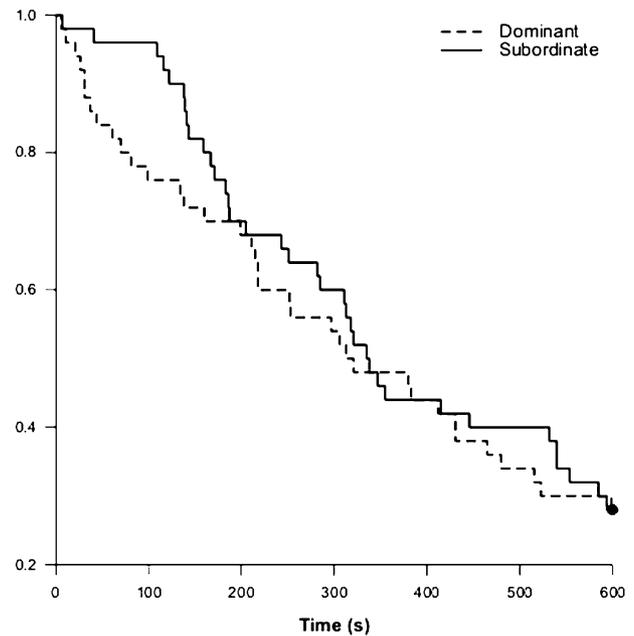


Figure 2. Data on latency to emerge from 0 to 600 s. Proportion of crickets still hiding vs. time (s) for dominant and subordinate *Gryllus integer* males in emergence trials. The male groups did not differ statistically significantly ($N = 100$, Gehan–Breslow test statistic = 0.626, d.f. = 1, two-tailed $P = 0.429$).

pared over the entire 600 s of the activity trials (Kaplan–Meier survival analysis, $N = 50$, Gehan–Breslow test statistic = 0.626, d.f. = 1, two-tailed $P = 0.429$; median of survival time = 335 s for subordinate; vs. 313 s for dominant; Fig. 2). However, in the first 200 s of the trials, dominant and subordinate males showed a statistically significant difference in the latency to emerge ('head out' times: Kaplan–Meier survival analysis, $N = 31$, Gehan–Breslow test statistic = 7.754, two-tailed $P = 0.005$; Fig. 3). Dominant males emerged more quickly from the refuge than subordinate males (median time for subordinate males = 44 s, median time for dominant males = 141 s). The distributions of emergence times over the entire 600 s for the two male groups showed that, although both groups contained a large proportion of males that hid for 600 s, a greater proportion of dominant males than subordinate males emerged in the first 100 s of the trials, and a greater proportion of subordinate males had intermediate and very long emergence times (Figs 4, 5).

DISCUSSION

In the present study, more aggressive, intrasexually dominant males became active more quickly than did their subordinate rivals when placed in a novel and

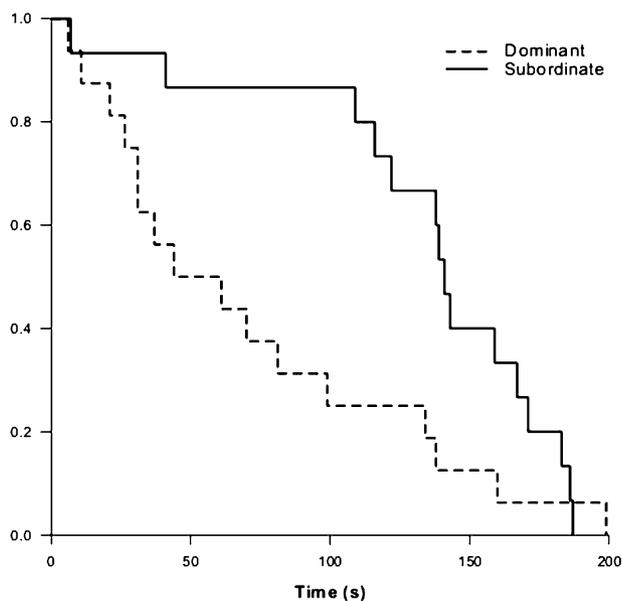


Figure 3. Data on latency to emerge from 0–200 s. Proportion of crickets still hiding vs. time (s) for dominant and subordinate *Gryllus integer* males in emergence trials. The male groups differed statistically significantly ($N = 31$, Gehan–Breslow test statistic = 7.754, d.f. = 1, two-tailed $P = 0.005$).

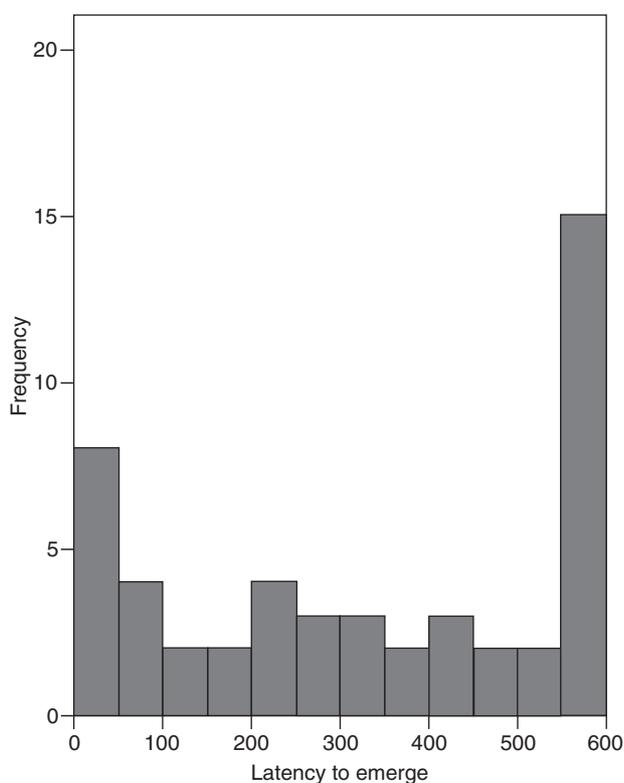


Figure 4. Dominant males. Histogram of data on latency to emerge from 0–600 s.

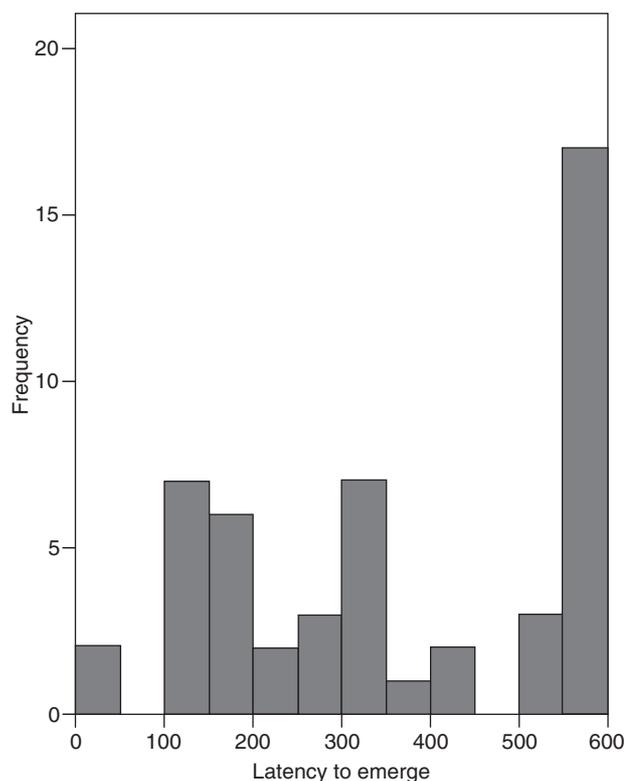


Figure 5. Subordinate males. Histogram of data on latency to emerge from 0–600 s.

potentially dangerous environment. In addition, a higher proportion of the more aggressive males (i.e. those that later won more fights than their opponents) emerged quickly from a refuge in a novel environment than less aggressive males. Together, these results suggest that there is an aggressiveness/activity behavioural syndrome in *G. integer*, in which more aggressive males are also more active in a novel environment, and more likely to be less ‘cautious’ with respect to predation risk. Similar aggressiveness/activity syndromes have been noted in other animals. For example, in great tits, individuals differ in their aggressiveness and their tendency to explore novel environments. This has been described as a ‘proactive–reactive’ syndrome, in which ‘proactive’ individuals are more aggressive and quicker to explore novel environments than ‘reactive’ individuals (Verbeek, Drent & Wiepkema *et al.*, 1994, Verbeek *et al.*, 1999). In chaffinches, activity levels are correlated with anti-predator behaviour: more active birds fly to escape models of predators, and have shorter latencies to return to previous activities after model presentation, whereas less active birds freeze when model predators are presented and have longer latencies to return to previous activities after model presentation (Quinn & Cresswell, 2005).

We believe that our measure of 'latency to emerge' quantifies variation in antipredator behaviour, rather than territoriality, because males never called from within the vial during our trials, suggesting that they did not treat it as a defensible resource. Similar hiding behaviour occurs in many taxa and it is generally recognized as an antipredator tactic (Dill & Fraser, 1997; Hugie, 2003; Jennions *et al.*, 2003; Hugie, 2004). Nonetheless, it is possible that subordinate males emerged more slowly than dominant males in our trials because they were taking more time to assess whether other males were nearby, or for alternative reasons.

Although our results suggest that more aggressive male crickets may be more conspicuous to predators because of their higher levels of activity, these individual differences in activity do not necessarily mean that aggressive males have a higher risk of predation. For example, more aggressive males might compensate behaviourally for greater conspicuousness (Hedrick, 2000). Even if more aggressive males are more conspicuous to predators, they might have traits such as faster reaction times, higher running velocity or longer escape runs than less aggressive males. More aggressive males should also be better at competing for a safe crack in the ground, from which male crickets call for mates. Thus, although behavioural syndromes may sometimes represent constraints on behaviour, explaining apparently 'non-adaptive' traits, the aggressiveness/activity syndrome in *G. integer* could instead represent an adaptive suite of characters (Sih *et al.*, 2004a,b). Our results in this species also may explain why pheromones from males with high fighting abilities were preferred by females in our previous tests of odour preferences (Kortet & Hedrick, 2005; but see also Shackleton, Jennions & Hunt, 2005): socially aggressive males may be more active, leaving abundant chemical cues for selective females (Kortet & Hedrick, 2005). A previous study by Hedrick (2000) of the population of *G. integer* in Davis, California, demonstrated that males with longer calls were more cautious: they had longer latencies to emerge from a refuge in a novel environment, and longer latencies to resume calling when interrupted by a predator cue. Unfortunately, in the present study, we did not measure male calling behaviour, and we do not know whether male aggressiveness is phenotypically linked with calling behaviour as well as 'cautiousness'. Further studies should help us to resolve this question.

Additionally, our research in a different population of *G. integer* in Arizona suggests that the latency to emerge from a refuge in a novel environment is related to predation risk: in Arizona, where predation pressure is very high, male *G. integer* have signifi-

cantly longer latencies to emerge than in California, where predation pressure is much lower (Hedrick & Kortet, 2006; see also Kortet, Rantala & Hedrick, 2007). We have not measured levels of intrasexual competition for mates in the Arizona population. However, if there is a general aggressiveness/activity behavioural syndrome in *G. integer* across populations (Bell, 2005), studies of aggressiveness in the Arizona population, in which crickets emerge slowly from refuges, should reveal that these crickets are less aggressive with one another than Davis crickets.

In conclusion, the Davis population of *G. integer* exhibits an aggressiveness/activity behavioural syndrome, such that males with higher fighting ability than their weight-matched rivals also have shorter latencies to become active in an unfamiliar environment, and often have shorter latencies to emerge into that environment from a refuge. These results suggest that the more aggressive males may be more 'bold' or incautious with respect to predation risk, and that there could be more than one adaptive strategy in this population. Future studies on this and other populations will address whether more active males are more conspicuous to predators, whether they can compensate for their presumably increased conspicuousness, whether calling characteristics are correlated with aggressiveness, as well as cautiousness towards predators, and whether the behavioural syndrome found here exists in other populations.

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