Dominance is not always an honest signal of male quality, but females may be able to detect the dishonesty

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Females prefer dominant males as mating partners in numerous species. Male dominance rank is considered as an honest signal of male quality, because only healthy males in good condition are thought to be able to win fights with other males. Here, we tested whether activation of the immune system influences the success of males in male–male competition and mating in the field cricket, *Gryllus integer*. We activated the immune system of males with a nylon monofilament (to mimic a parasitoid larva), and arranged fights between male pairs to assess male dominance and associated mating success. Activation of the immune system with nylon monofilament substantially enhanced the fighting success of males during male–male competition but had no effect on mating success. However, sham-manipulation (a wound only) did not have any effect on fighting success although females mated more often with dominant males. Our study suggests that when male crickets meet an apparent survival threat they may behave more dominantly, probably owing to terminal investment. Male success during male–male competition is not always an honest signal of males’ quality, but females may be able to detect this dishonesty.

1. Introduction

Dominant behaviour during male–male competition may increase males’ chances of mating with females [1]. Female preferences for dominant males can provide various direct benefits for choosy females and their offspring [2]. However, even in mating systems such as leks, where females do not receive any direct benefits, they often prefer dominant males as mates [2]. Thus, it has generally been thought that by preferring dominant males as mates, females are also choosing ‘good genes’ for their offspring, as dominance should be an honest signal of male quality [3]. However, the mechanism for maintaining honesty is less clear. According to the immunocompetence handicap hypothesis, males may vary in their ability to withstand the costs of dominance and immune function, so that only high-quality males can maintain both high dominance rank and effective immune function [2,4,5].

Previous studies have proposed that male dominance status per se could be equivalent to a sexual ornament [6–8] and it is often positively associated with other forms of sexual advertising [7,9–11]. Female crickets use male calling and courtship songs as criteria when choosing mates. Males with attractive calling or courtship songs have stronger immune defence than males with less attractive songs [12]. Unfortunately, male calling song also attracts an acoustically oriented lethal parasitoid fly, *Ormia olcens*, which deposits its larvae on the cricket [13]. Pathogens and the artificial activation of insect immune systems have been found to reduce sexual signalling [14], probably by reducing the general condition of individuals. On the other hand, according to previous studies,
activation of the immune system might cause males to invest more in sexual signalling as a terminal investment in reproduction [15,16]. Thus, it might be that sexual signalling is not always an honest signal of male quality or health. However, to the best of our knowledge, no previous studies have tested whether activation of an insect immune system with a potentially lethal intruder causes behavioural terminal investment in male–male competition and whether it has an effect on male’s mating success. According to the hypothesis of terminal investment, individuals should invest more in present reproduction when there is a serious risk of dying soon [17].

To test whether activation of the immune system has an effect on the outcome of male–male competition and mating success, we used the field cricket Gryllus integer (Orthoptera: Gryllidae; Scudder, 1901) as a model. In Gryllus crickets, females actively mount males to copulate; as a consequence, the chance of forced mating by a male is very low [18]. Gryllus females also prefer dominant males as mates [7]. Recent studies on other crickets indicate that dominant males have stronger immune systems than subordinate males [7,9]. Here, we tested the effect of immune activation on male behaviour during male–male competition and on associated mating success. We hypothesized that activation of the immune system with an artificial parasitoid larva would lead to terminal investment. If so, males with activated immunity should behave more aggressively to increase their potential reproductive success.

2. Material and methods

(a) Study animals

Our study animals were descendants of wild crickets (collected in Davis, CA, USA in 2008) that were maintained at the University of Turku, Finland. Crickets were kept in large plastic boxes (28 ± 1 °C, 12 L : 12 D cycle) containing water, cabbage, protein chow and a carton for hiding. From the stocks, we collected juvenile crickets before their final eclosion and transferred them individually to covered 1 l plastic vials containing water, food (ad libitum) and a cover. Crickets were physically isolated to ensure virginity and to control for experience.

(b) Male pairs and treatments

The crickets were used in the experiment 7–19 days after they reached maturity. Individuals missing body parts were excluded. First, we weighed the fresh body mass of males to the nearest 0.1 mg to produce weight-matched male pairs (6% difference in weight allowed) of the same age (± 1 day). We had two immune manipulation treatment groups. In one, a randomly selected male from each pair was treated with an inserted implant (63 pairs). In the other, a randomly selected male in each pair (34 pairs) was given a wound with a sterile needle (sham-manipulation). The remaining male in all pairs was not manipulated but was otherwise treated similarly (treatment control). Both immune manipulation treatments were applied on the left side of the cricket through a puncture in the pleural membrane between the second and third sternite [7]. Before manipulations, males were anaesthetized with carbon dioxide. Implants were 4 mm long pieces of nylon monofilament (diameter 0.18 mm). Finally, we painted a red spot on one side of the pronotum of both the males allow individual identification during the trial. After the immune manipulations, crickets had no access to food.

3. Results

During the fight trials, one of the males always achieved dominance over the other. Males whose immunity had been activated with nylon monofilament implants won 46 of 63 fight trials, whereas treatment control males won only 17 trials (figure 1). By contrast, sham-manipulated males (wounded only) won 16 of 34 fight trials, whereas treatment control males won 18 (figure 1). Immune activation with implants apparently increased male fighting success (chi-square test, \( n = 97, \chi^2 = 6.451, p = 0.011 \)).

Among sham-manipulated males, females refused to mate with four male pairs of 34, whereas among implanted males females refused to mate with 26 male pairs of 63 (chi-square test, \( n = 97, \chi^2 = 8.999, p = 0.003 \)). There were no differences in mating success when comparing dominant implanted males and dominant sham-manipulated males with subordinate males (chi-square test, \( n = 67, \chi^2 = 2.395, p = 0.122 \)). In the sham-manipulation trials, the dominant males were more successful in obtaining copulations in 21 trials of 30, whereas subordinate males were more successful in obtaining copulations in nine trials (figure 2; chi-square test, \( n = 60, \chi^2 = 9.600, p = 0.002 \)). By contrast, in the implant trials, there were no differences: dominant males were more successful in mating in 19 trials of 37, versus subordinate males in 18 trials (figure 2; chi-square test, \( n = 74, \chi^2 = 0.054, p = 0.816 \)).
However, there were no differences in mating success between sham-manipulated and implanted males (chi-square test, \( n = 67 \), \( \chi^2 = 0.304, \ p = 0.581 \)). Sham-manipulated males managed to mate with 15 females of 30, whereas treatment control males managed to mate with 15 females. Similarly, implanted males managed to mate with 16 females of 37, whereas treatment controls mated with 21 females.

### 4. Discussion

Our study shows that males whose immune systems were activated with a nylon monofilament implant were more successful at winning fighting trials than sham-manipulated males. On the basis of these results, it is possible that in the face of certain death, by activating terminal investment of body resources and efforts, males may behave more aggressively as a final attempt to increase fitness. Importantly, our results suggest that success in male–male competition is not always an honest signal of male quality. Recent studies propose that secondary sexual characters such as the calls and courtship songs of field crickets are a reliable indicator of male quality or pathogen resistance [10,12]. In *G. integer*, females prefer pheromones of dominant males [10], indicating that male quality and secondary sexual characters may be coupled with male dominance. By investing more in male–male competition, males may improve their chances of copulating with females and thereby increase their own fitness. In our study, females preferred dominant males as mates only in sham-manipulated trials suggesting that females are able to detect when males signal dominance dishonestly. Additionally, mating success overall was lower in the group of implanted males compared with the sham-manipulation group. It seems that females do not prefer male dominance *per se* but instead other, maybe chemical, traits that are associated with dominance and mating success.

In previous studies, immune activation negatively affected the condition or survivorship of individuals. For example, in the yellow meal worm, *Tenebrio molitor*, implantation shortened an individual’s lifespan [19]. Similarly, lipopolysaccharide injections administered to bumblebee workers (*Bombus terrestris*) reduced their survival under starvation [20]. Thus, it seems that in insects the harmfulness of pathogenic infection might be owing to activation of the immune system *per se* [14]. Our data suggest that immune activation with a nylon monofilament implant can be a plausible method for activating terminal investment in *G. integer* although it was not independently tested here.

To conclude, the present data are, to our knowledge, the first to demonstrate enhanced fighting success after serious risk of death as a possible behavioural terminal investment. Furthermore, our results show that females may be able to detect when males signal dominance dishonestly. Here, we have used relatively young, age-matched pairs although the strength of the terminal investment might vary during life-span. We encourage further research of this interesting topic to evaluate generalization of the observed results.

We thank all the people in the laboratory for assistance. This study was supported by the Turku University Foundation and the Finnish Cultural Foundation support to M.P., and the Academy of Finland to M.J.R. and R.K. (project no. 127398) and by the National Science Foundation to A.H. (IOS-0716332).

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