Male dominance determines female egg laying rate in crickets

Amanda Bretman[1,2,*],
Rolando Rodríguez-Muñoz[1,2]
and Tom Tregenza[1,2]

[1]*Centre for Ecology and Conservation, University of Exeter, Cornwall Campus, Tremough, Penryn TR10 9EZ, UK*
[2]*School of Biology, University of Leeds, Leeds LS2 9JT, UK*
Author for correspondence: Centre for Ecology and Conservation, University of Exeter, Cornwall Campus, Tremough, Penryn TR10 9EZ, UK (a.j.bretman@ex.ac.uk).

A key prediction of theories of differential allocation and sexual conflict is that male phenotype will affect resource allocation by females. Females may adaptively increase investment in offspring when mated to high quality males to enhance the quality of their offspring, or males may vary in their ability to manipulate female investment post-mating. Males are known to be able to influence female reproductive investment, but the male traits underlying this ability have been little studied in taxa other than birds. We investigated the relationship between male dominance and female oviposition rate in two separate experiments using the field cricket, *Gryllus bimaculatus*. In both experiments, females mated to more dominant (but not larger) males laid more eggs. This reveals that either females allocate more effort to reproduction after mating with a dominant male or that dominance status is associated with male ability to manipulate their mates. This is the first evidence that dominance, rather than male attractiveness, has a post-copulatory effect on reproductive investment by females.

Keywords: sexual selection; fighting; Acp; parental investment; female choice

1. INTRODUCTION

Females frequently exercise choice over mating partners and may also exert post-copulatory control over offspring paternity (Eberhard 1996). Additionally, Burley (1988) proposed that selection would favour females that could differentially allocate their resources according to the quality of their mates, thus enhancing female inclusive fitness through increasing the fitness of all offspring or the attractiveness of sons. Studies that support the differential allocation hypothesis come from various taxa (discussed by Sheldon 2000) including insects (for example, Arnqvist & Danielsson 1999; Kotiaho *et al.* 2003). Alternatively, males of several species are known to be able to stimulate oviposition (discussed by Eberhard 1996) and male *Drosophila melanogaster* produce accessory gland proteins that can increase oviposition rate even at a cost to females (Fowler & Partridge 1989; Chapman *et al.* 1995).

If females allocate resources differentially according to the quality of their mates, this must be associated with some male trait that indicates genetic quality. It has been proposed that dominance demonstrates male quality and even that females may incite fights to judge the best sires (Cox & LeBoeuf 1977; Berglund *et al.* 1996). In the field cricket *Gryllus bimaculatus* (De Geer), dominance has been demonstrated to be important pre-copulation through male–male competition for access to females and female choice (Simmons 1991; Wedell & Tregenza 1999; Rantala & Kortet 2004), but the post-copulatory effects of dominance have not been studied. In two separate experiments (the second as a further test of the relationship found in the first), we assessed male dominance over a series of fights and its relationship with oviposition rate of their mates. If females adaptively increase investment in offspring when mated to dominant males, or male ability to manipulate female investment post-mating is related to dominance, we expect females mated to more dominant males to increase oviposition rate.

2. MATERIAL AND METHODS

Stocks for both experiments were the descendents of individuals caught near Sevilla, Spain in 2003. Crickets were separated into single sex stock boxes as late instar larvae, so were naive to adults of the opposite sex. Adults were removed daily and housed individually. Virgin females were mated 9 days after eclosion. Mates were assigned randomly. As females do not lay particularly discrete clutches, eggs were removed and counted twice so that each female had two measures of egg number; in experiment A, 5 days after mating (referred to as days 1–5) and again 9 days later (days 5–14), in experiment B, 7 days after mating (days 1–7) and again 7 days later (days 7–14). This difference in timing of egg collection was for logistical reasons. Data were analysed as eggs per day (total number of eggs/number of days).

Virgin males were divided into experimental males or opponents 8 days after eclosion. Experimental males were immediately mated and then marked on the pronotum with a small spot of correction fluid, for individual recognition in dominance trials. Male dominance was assessed by placing experimental males in sequential contests with different opponents, four contests in experiment A, six in experiment B (to provide a more accurate measure of dominance). Experimental males' contests commenced 24 h after mating, and were repeated at 24 h intervals; this interval removes the effect of prior experience (Khazraïe & Campan 1999). Fighting in *G. bimaculatus* follows a stereotyped pattern and the winner is easily determined (Adamo & Hoy 1995). In experiment A, 118 experimental males were tested, 140 in experiment B.

Pronotum width of all individuals was measured after males had completed contests and after the oviposition period for females. Pronotum width is highly correlated with other measures of body size and mass, but is not prone to the changes that can occur in body mass over time (Simmons 1986).

Data were analysed separately for each experiment using SPSS v. 11.0. Previous studies of *G. bimaculatus* have found that dominance is affected by size, but size is not the sole factor determining dominance (Wedell & Tregenza 1999; Hofmann & Schildberger 2001). To control for the size difference between experimental males and opponents, dominance was calculated using the standardized residuals from a logistic regression of the relative size of pairs (experimental male size − opponent size) on the win or loss by the experimental male. This had the effect of an experimental male receiving a higher score if he won when he was smaller than the opponent than if he won but was larger. Scores were summed to give each experimental male a score across all his fights.

For experiment A, the data were analysed using a general linear model (GLM), with the response variable of number of eggs laid per day square root transformed to achieve normality. Oviposition period was a factor; dominance score, female size and male size were covariates. All interactions were tested and non-significant terms were removed in a backwards stepwise procedure. For experiment B, the data could not be analysed in one GLM, since it was not possible to transform the number of eggs laid data from days 7 to 14 due to the high number of females (30%) that did not lay any eggs during this period. A logistic regression of laying or not
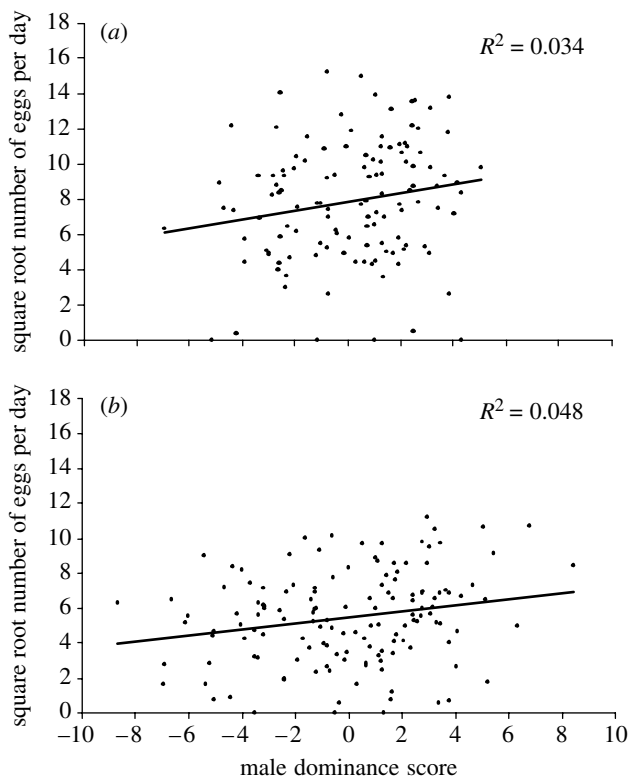
Figure 1. Number of eggs laid per day by a female in relation to the dominance score of her mate from (*a*) experiment A days 5–14 and (*b*) experiment B days 1–7. Number of eggs was square root transformed. Dominance score was the sum across fights for each male of the residuals from a logistic regression of relative size of combatants on win/loss of the experimental male. Regression line is the best fit to the data, R^2 values are given.

laying eggs on dominance score was marginally non-significant (Wald = 2.77, $p = 0.09$), hence it would be inappropriate to remove the data from females that did not lay any eggs. Data for days 1–7 were analysed with a GLM as for experiment A; days 7–14 with a Spearman rank correlation.

3. RESULTS
(a) *Experiment A*
Females mated to more dominant males laid more eggs per day ($F_{1, 231}$ $F = 5.57$, $p = 0.02$). The effect of size of either sex was not significant (female $F_{1, 231}$ $F = 2.39$, $p = 0.12$; male $F_{1, 231}$ $F = 0.08$, $p = 0.37$). There were no significant interactions. The effect of oviposition period was marginally non-significant (days 1–5 or days 5–14, $F_{1, 231}$ $F = 3.63$, $p = 0.06$) and *post hoc* tests revealed that the effect of dominance on egg number was significant only in the days 5–14 period (days 1–5 $F_{1, 116} = 1.31$, $p = 0.26$; days 5–14 $F_{1, 116} = 5.27$, $p = 0.02$, figure 1*a*).

(b) *Experiment B*
In days 1–7, females mated to more dominant males laid more eggs per day ($F_{1, 135} = 6.97$, $p = 0.009$, figure 1*b*), again controlling for female size ($F_{1, 135} = 11.10$, $p = 0.001$) and male size ($F_{1, 135} = 0.67$, $p = 0.42$). Data from days 7 to 14 revealed no relationship between egg number and dominance (Spearman, $n = 140$, $r_s = 0.052$, $p = 0.54$).

4. DISCUSSION
We have shown that female field crickets mated to more dominant males laid more eggs. This relationship was significant while controlling for female and male size and relative size of opponents. Although the variance in egg number explained by dominance was small at between 3 and 5% (figure 1), it was the only predictor that was significant in both experiments. The pattern observed can be explained by two processes; females may adaptively increase oviposition rate when mated to more dominant males, or male ability to manipulate female oviposition rate may be related to dominance. Our experiments differ in when the increase in oviposition was apparent, in experiment A at days 5–14 and experiment B at days 1–7. This suggests that the crucial period was between the fifth and seventh days after mating, which coincides with the period of maximum oviposition rate in *G. bimaculatus* (Simmons 1988). A previous study of *G. bimaculatus* found that females allowed to choose mates laid more eggs (Simmons 1987), however, as females in the choice treatment were allowed to mate polyandrously, whereas all other treatments were not, it is unclear whether this was an effect of male attractiveness or polyandry *per se*, or a combination of the two.

If variation in oviposition rate with respect to male phenotype is adaptive for females, they must gain some benefit from increased reproductive effort when mated to dominant males. Previous work on *G. bimaculatus* has demonstrated that mating success of sires (assessed to include both male dominance and female choice) predicts that of sons (Wedell & Tregenza 1999). Hence, females may be able to increase their number of dominant sons by increasing oviposition rate after mating with dominant males. Rantala & Kortet (2004) also found that dominant males were more successful at gaining copulations and that more dominant males had better immune responses, suggesting that dominance may be correlated with other measures of male quality. This would benefit both male and female offspring and hence females could increase their fitness by laying as many eggs as possible, in keeping with Burley's (1988) predictions. In our study, females did not witness male–male competition, so fights could not directly stimulate oviposition rate. Male pheromones could provide an oviposition stimulus, for example *G. integer* females prefer the scent of dominant males (Kortet & Hedrick 2005).

Males can influence fecundity by providing food to the female in the form of nuptial gifts such as a spermatophylax or the ejaculate itself, so directly contributing nutrients to provision eggs (Gwynne 1988; Savalli & Fox 1997). However, the *G. bimaculatus* spermatophore is small and whether or not females eat it has no effect on fecundity (Simmons 1988). Male seminal products can stimulate oviposition, for example accessory gland proteins that increase oviposition have been identified in flies (Chapman *et al.* 1995) and prostaglandins have a similar effect in crickets (Stanley-Samuelson *et al.* 1987). Our findings could be explained if dominant males generate more prostaglandin than subordinate males. It has yet to be shown that

G. bimaculatus produce prostaglandins with this effect, but previous work suggests that male *G. bimaculatus* have some influence over female oviposition and re-mating rate and points to the spermatophore as the source of these effects (Orshan & Pener 1991; Loher *et al*. 1993).

Our study demonstrates that male dominance influences oviposition rate while male size does not. Whether this is directly advantageous to females (high oviposition rates may increase reproductive success), or indirectly advantageous (they have more offspring inheriting genes associated with dominance), or whether it is advantageous to males but detrimental to females because females that lay many eggs rapidly have fewer offspring overall, requires further study.

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