



## The effects of male phenotypic condition on reproductive output in a sex role-reversed beetle



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In insects with sex role reversal in mating, in which females actively court males, large and nutritious ejaculates are a common direct benefit to females. Such ejaculates are costly for males to produce and their size and composition can depend on male condition. However, the fitness effects to males and females of such condition-dependent provisioning are less clear. Here, we studied the effects of phenotypic condition on mating behaviour, ejaculate size and reproductive output in honeylocust beetles, *Megabruichidius dorsalis*. Our experimental design allowed us to disentangle the independent effects of juvenile resource acquisition in both sexes (as reflected by body size) and resource acquisition by adult males (feeding). We show that phenotypic condition of both sexes had sizeable independent and interactive effects on mating and reproductive output. In males, resources accrued during the juvenile phase had significant but relatively marginal effects on male mating and reproduction. Male adult feeding, in contrast, had sizeable effects on almost all aspects of male and female reproduction, through the nutritional effects of ejaculates in females. We discuss our findings in light of the reversal of both sex roles and sexual size dimorphism exhibited by this species, relative to related species. Our results highlight the importance of testing the interaction of male and female condition on components of fitness to understand the evolution and maintenance of mating systems.

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In most animal species, sexual selection is stronger in males than in females as an indirect consequence of anisogamy (Bateman, 1948; Schärer, Rowe, & Arnqvist, 2012). Females produce large, costly eggs, which are typically produced at a slower rate than smaller, less costly sperm (Hayward & Gillooly, 2011). The reproductive rate of females is thus typically limited by egg production, while males are often limited by the number of eggs they fertilize (Bateman, 1948; Trivers, 1972). In contrast to this typical scenario, stronger sexual selection in females can occur when males provide females with substantial direct benefits, most commonly in the form of parental care, nuptial gifts or access to territories (Berglund & Rosenqvist, 1993; Fritzsche & Arnqvist, 2013; Gwynne, 1986; Takakura, 1999; Vahed, 1998). In this case, a male's reproductive success may not primarily be limited by his mating rate, but rather by his ability to provide such benefits (Proctor, 1992; Simmons, 1995; Simmons & Kvarnemo, 1997).

Large, nutritious ejaculates are a common direct benefit to females in insects (Choe & Crespi, 1997; Thornhill & Alcock, 1983). These ejaculates are costly for males to produce and their size and composition can depend on male condition (Boggs, 1990; Dewsbury, 1982; Gwynne, 1984, 1988; Moya-Larano & Fox, 2006; Reinhardt, Naylor, & Siva-Jothy, 2009; Thornhill, 1976; Ursprung, den Hollander, & Gwynne, 2009). Two main factors have been shown to influence the characteristics of such ejaculates. First, ejaculate size and composition often increase with male body size, analogously to the effects of size on fecundity in females (Jia, Jiang, & Sakaluk, 2000). Second, ejaculates can be affected by environmental conditions, particularly the availability and quality of food resources (Gwynne & Simmons, 1990; Perry & Rowe, 2010; Proctor, 1992). In katydids, for example, food shortage results in fewer sexually active males and smaller nutritious spermatophores among those males (Gwynne, 1993; Jia et al., 2000).

Male provisioning of direct benefits can select for multiple mating in females (polyandry) and for female choice of males that provide greater benefits. This can subsequently generate selection on males to provide greater benefits in order to attract females or to induce resistance to further mating in females (Arnqvist & Nilsson, 2000; Gwynne, 1990; Jennions & Petrie, 2000; Simmons, 2005;

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Simmons & Bailey, 1990; Wedell, 1996). Female choice for large males has been documented in several gift-giving insects. For example, female choice for large males in ground crickets generates direct sexual selection on male body size (Fedorka & Mousseau, 2002a). Males may thus evolve to exceed females in body size in gift-giving taxa (Bonduriansky, Wheeler, & Rowe, 2005), even in groups such as insects in which females are normally larger than males (Savalli & Fox, 1999; Ursprung et al., 2009).

However, the effects of male condition-dependent ejaculate characteristics on male and female fitness are not well understood (Fedorka & Mousseau, 2002a; Perry & Rowe, 2010). To study strategic ejaculate allocation, some studies have manipulated female condition and investigated the effects on male ejaculates and on females only (Bonduriansky et al., 2005; Fox, 1993; Takakura, 2004). Other studies have manipulated male condition but have focused strictly on ejaculate traits rather than male reproductive output (Perry & Rowe, 2010; Proctor, 1992). In this study, we aimed to provide a complementary contribution by investigating how the availability of food to males interacts with male and female body size to determine mating behaviour and reproductive outcome for both sexes in a role-reversed and gift-giving mating system.

In the sex role-reversed honeylocust beetle, *Megabruchidius dorsalis* (Bruchinae), males transfer an ejaculate that comprises some 5–12% of their body weight, which exceeds that in related seed beetle species (Rönn, Katvala, & Arnqvist, 2008; Takakura, 1999). Mating carries substantial costs to males (Salehialavi, Fritzsche, & Arnqvist, 2011). In contrast, females gain substantial direct benefits from mating and female offspring production increases with each additional mating (Takakura, 1999). Females have evolved to actively court males (Fritzsche & Arnqvist, 2013; Salehialavi et al., 2011; Takakura, 1999, 2006). Previous work has shown that male condition markedly affects the magnitude of direct benefits to females. Females mated to well-fed males lay larger eggs, produce offspring that perform better, and show reduced feeding behaviour in comparison to females mated with poorly fed males (Takakura, 2004). Females also prefer to mate with larger males, suggesting that direct benefits are larger when mating with large males (Salehialavi et al., 2011; Takakura, 2004).

Here, we assessed how body size of both females and males interacts with adult male food provisioning to influence mating success and reproductive output in this sex role-reversed mating system. We hypothesized that male size is under fecundity selection and that the nutritional value of a male's ejaculate is condition dependent, such that ejaculate weight is influenced by both juvenile and adult resource acquisition. Our design allowed us to separate effects of male resource acquisition during the juvenile phase (manifested as adult body size) from those that result from male resource acquisition during the adult stage. We predicted that (1) larger and better-fed males would transfer larger and more nutritious ejaculates and (2) females mated to such males would produce more offspring than those mated to small and/or poorly fed males, resulting in higher reproductive success for both these females and their mates, (3) mating behaviour of both sexes would depend on male size and feeding status and (4) the absolute reproductive benefits to females from receiving nutritious ejaculates should depend on female body size.

## METHODS

### *Model Organism and Experimental Design*

Honeylocust beetles were kept on seeds of *Gleditsia triacanthos* in 1-litre glass containers in climate chambers set to 26 °C, 70 ± 10%

relative humidity with a 16:8 h light:dark cycle. Under these conditions generation times are approximately 7 weeks. Virgin individuals were obtained by isolating single beans, each containing a single larva, in 24-well culture plates. Individual beetles were collected on 9 consecutive days directly after hatching and kept in petri dishes in same-sex groups (10 individuals).

All beetles were then weighed to the nearest µg using a microbalance (Sartorius Genius ME 235P). Individuals of both sexes were then selected from two weight classes: 'large' individuals were those in the upper 30 percentile of the weight distribution for their sex and 'small' individuals were those in the lower 30 percentile of the weight distribution. Individuals of each weight class and feeding treatment (for males; see below) were then randomly assigned to one of eight different mating treatments using a fully crossed 2 × 2 × 2 design with nine or 10 replicates per cell. The three factors were male food treatment (fed versus non-fed), male size (large versus small) and female size (large versus small). In total 77 pairs of beetles were observed in repeated mating trials. To assess virgin life span, additional virgin individuals of both sexes were kept separately in petri dishes, replicated 8–10 times for each food treatment and size group.

To assess the effects of food provisioning to adult males, half of all males in each size class were provided with water, 20% sucrose solution and pollen (Bee Pollen Capsules, Manuka Health Ltd., New Zealand) while the other half were provided with water only. All females were provided with water only. We refer to the two male groups as the nonfed and fed male treatments, respectively. This feeding regime was maintained until the onset of the experiments (16 days). After the start of the mating experiment, all beetles were provided with water only.

### *Mating Trials*

Our primary goal was to measure reproductive productivity of each male–female pair. Each pair was thus placed in a 3 cm petri dish and observed until a mating was completed, or for a maximum of 30 min if no mating commenced during this time. Pairs were then separated. The same pair was placed together again for a second trial after 24 h and a third trial after 48 h. The time period between matings was chosen to match the period males need in order to replenish their ejaculate (Salehialavi et al., 2011). Thus each pair could mate a maximum of three times over 3 consecutive days. To estimate the amount of absolute and relative ejaculate transferred during mating, both males and females were weighed immediately before and after each mating. Absolute ejaculate weight was calculated as the difference in male body weight before and after mating and relative ejaculate weight was calculated by dividing absolute ejaculate weight by body weight before mating.

In between and after mating trials, males were kept individually in plastic petri dishes and provided with water. Females were kept individually in glass petri dishes (12 cm) provided with water and 100 g of *Gleditsia* beans as an ad libitum substrate for oviposition. Larvae bore into a bean upon hatching, where they complete their development and emerge as adults. After the third mating trial, females and males were kept in their individual petri dishes until death and their life span was recorded. The beans in the female petri dishes were subsequently incubated in climate chambers until all offspring hatched and the number of offspring of each pair was recorded, as an estimate of their joint reproductive output.

### *Ethical Note*

The honeylocust beetles used to conduct this experiment originated from field samples taken at Inogashira Park, Tokyo, Japan.

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