

The interplay between different stages of reproduction in males of the moth *Plodia interpunctella*



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As a result of female remating, sexual selection can operate both before and after copulation, yet studies of sexual selection on males tend to focus on individual episodes of reproduction in isolation. We examined whether different episodes of sexual selection are related in the sperm-polymorphic Indian meal moth, *Plodia interpunctella*. We found that the ability to mate with nonvirgin females determined male precopulatory reproductive success. In addition, males that transferred more sperm during their first mating were better at both sperm competition and reducing females' propensity to remate, suggesting that sperm production and transfer are key determinants of reproductive success in this species. However, no relationships were found between traits contributing to pre- versus postcopulatory sexual selection. Our results illustrate the importance of considering variation in all aspects of male reproductive success when examining sexual selection.

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It is now generally accepted that sexual selection operating on males occurs not only prior to copulation, but also after copulation in the form of sperm competition and/or cryptic female choice (reviewed in Birkhead & Møller 1998). Despite the wealth of studies examining the evolution of traits under pre- versus postcopulatory sexual selection, our understanding of the relationship between different stages of reproduction is still limited. Yet determining whether male traits are subject to similar or divergent selection pressures during different stages of reproduction is important for our understanding of how total sexual selection operates on males (Hunt et al. 2009). Each different stage of reproduction might intrinsically increase or decrease the variance in male reproductive success, thereby amplifying or dampening variance in overall reproductive success.

Attractive males that are preferred by females have been shown to exhibit higher fertilization success than nonpreferred males in *Drosophila simulans* (Hosken et al. 2008), *Drosophila melanogaster* (Bretman et al. 2009; Fricke et al. 2010) and the guppy, *Poecilia reticulata* (Evans et al. 2003; but see Evans & Rutstein 2008). In *D. melanogaster* and the dung fly, *Scathophaga stercoraria*, males that exhibit high sperm competitive success also produce offspring of higher viability (Hosken et al. 2003; Droge-Young et al. 2012). In

the web-building spider *Stegodyphus lineatus*, large males are more successful at fighting, and are also better at coercing nonvirgin females into mating (Maklakov et al. 2004). These studies suggest that in some species, the different stages of reproduction act in concert to favour intrinsically superior males. In contrast, other studies have reported that different reproductive events can counteract one another's contribution to variation in reproductive success. In the water strider, *Gerris lacustris*, large males are more attractive to females and thus have higher mating success, but small males copulate for longer and have higher fertilization success at each mating (Danielsson 2001). Potentially this is the result of a trade-off between mating frequency and sperm production in this species. Similarly in scorpionflies (Engqvist 2011), fireflies (Demery & Lewis 2007; South & Lewis 2012), orb-weaver spiders (Schneider & Elgar 2005) and midges (Neems et al. 1998), different stages of reproduction counteract one another, thereby decreasing the variation in male reproductive success. Although these studies provide insights into how sexual selection influences male reproductive success both before and after copulation, and how different episodes of sexual selection might interact, there have been few studies examining all episodes of sexual selection in the same individual (e.g. Pischedda & Rice 2012), partly as a result of the difficulties associated with tracking all stages of reproduction throughout an individual's lifetime (Droge-Young et al. 2012).

We examined different stages of male reproduction in the Indian meal moth, *Plodia interpunctella*, and the relationships

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between them. A previous study showed that male precopulatory mating success is positively related to development time and adult longevity in this species (Lewis et al. 2011). However, the relationships between precopulatory mating success and other stages of reproduction are unknown. Female *P. interpunctella* can mate up to five times over the course of their adult life span, but typically only mate about twice (Cook & Gage 1995; Cook 1999). Therefore, in the wild, many of the females a male encounters are likely to be nonvirgin. In the current study we measured precopulatory reproductive success not only as lifetime number of matings, but also as the ability of males to 'seduce' (i.e. successfully court and mate) an already mated female. If certain males are intrinsically more attractive to females than other males, and thus favoured regardless of female mating status, we might predict that preferred males will both have greater ability to copulate with previously mated females and achieve a higher lifetime number of matings.

We measured postcopulatory reproductive success as fertilization success when a male's sperm competes against the sperm of a rival male. When two *P. interpunctella* males mate with the same female, the second male tends to fertilize the majority of the female's offspring, and this variation is thought to be dependent on ejaculate size (Cook et al. 1997). However, it is unknown whether there is a relationship between males' sperm competitive ability, and their ability to obtain matings. In many species males can also increase their postcopulatory reproductive success by suppressing female receptivity postmating; in this way males can avoid or reduce sperm competition altogether (reviewed in Simmons 2001). In the Lepidoptera, the ability to suppress female remating is thought to be related to ejaculate size and number of nonfertile sperm transferred (Cook & Wedell 1999). We therefore also measured males' ability to suppress females' remating in *P. interpunctella*.

METHODS

Rearing of Experimental Stock

A large stock population of *P. interpunctella* was cultured using individuals collected in Perth, Australia in 2001. Larvae were reared on a diet of bran midlings, yeast, honey and glycerol, at a

temperature of $28 \pm 3^\circ\text{C}$ with a 16:8 h light:dark photoperiod (Gage & Cook 1994). Effects of larval crowding were removed by rearing larvae with excess food at constant densities: 400 ml of medium per 100 eggs. The experiment required virgin adults of known age. Therefore, before the experiment individual fifth-instar larvae were isolated from the stock population in 10 ml vials containing a small quantity of larval medium. All experiments took place during the 8 h dark phase of the light cycle. In addition to the wild-type individuals, we used a recessive golden body colour mutant marker of *P. interpunctella* (Beeman & Schmidt 1982; Beeman 1983). These individuals were reared under the conditions detailed above. Only variation in postcopulatory success between wild-type (focal) males was compared, as sperm competitive abilities between the wild type and golden mutant differ (see Results). Thus the golden males were only utilized as standardized competitors.

Precopulatory Reproductive Success and Sperm Transfer

The experimental design is illustrated in Fig. 1. Approximately 150 freshly emerged virgin focal wild-type males and 150 freshly emerged virgin golden males were individually placed in 30 ml vials with a virgin golden female. Each subsequent day of his adult life, each focal wild-type male was presented with a new female, either virgin or previously mated to a golden male (see next section on estimating male postcopulatory reproductive success), for the length of the 8 h dark phase of the light cycle, and it was noted whether copulation occurred. Matings were conducted in a dark room lit with a dull red lamp to allow observation. This continued until death of the male, whereupon adult longevity and total number of matings were noted. Males live on average 8 days in this species (Lewis et al. 2011). Total number of matings, plus the ability to copulate successfully with an already mated female, was taken as an indication of lifetime precopulatory mating success.

The number of sperm males transferred in the spermatophore was estimated for each male on his first mating. This was then used as a proxy for sperm numbers transferred in subsequent ejaculations, as in this species there is a correlation between sperm investment in first and second matings (regression: $y = 0.599x + 3359$, $F_{1,14} = 5.97$,

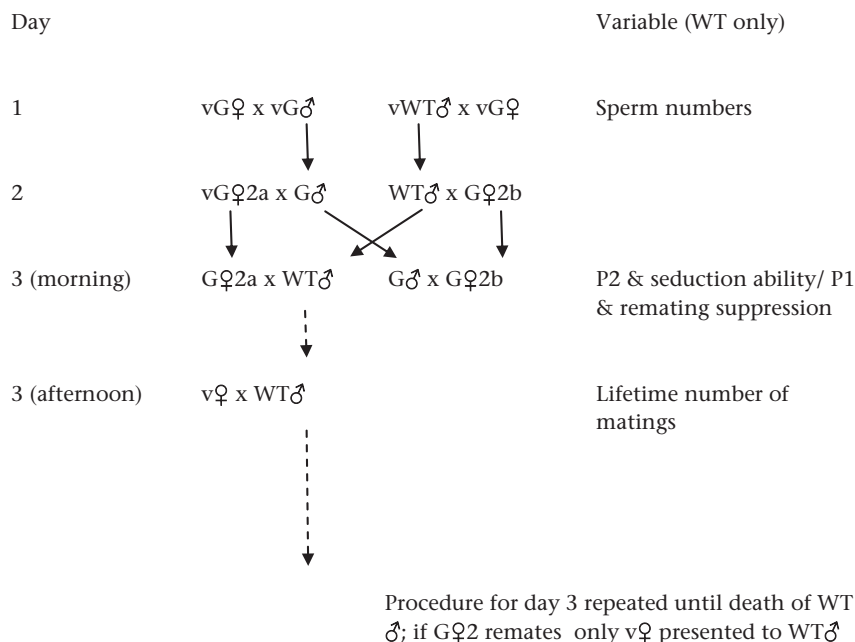


Figure 1. Experimental design: v = virgin; WT = focal wild type; G = standardized golden competitor.

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