



The fitness cost to females of exposure to males does not depend on water availability in seed beetles

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Access to multiple males can benefit a female in terms of increased fecundity and/or offspring performance. However, the presence of more males can also impose costs on females that arise from an elevated mating rate (e.g. due to increased genital damage, loss of feeding opportunities) and/or increased harassment. Different environments might influence the relative magnitude of these costs and benefits, because they can influence how often males and females encounter each other as well as the nature of these encounters. In the seed beetle, *Callosobruchus maculatus*, water is a limiting resource for females that can be obtained from male ejaculates. Here we explored whether the net fitness of female seed beetles is affected by breeding in either a dry or a wet environment when housed with differing numbers of males (none, one or four). Consistent with costly male harassment, females housed with four males laid significantly fewer eggs than those housed alone or with a single male, but there was no effect of the number of males on female egg-laying rate, life span, larval development rate or egg–adult survival of offspring. Although females in the wet environment lived significantly longer, there was only tentative evidence that water availability affected the net fitness cost to females of being exposed to more males. We conclude that to understand the evolution of mating systems it is important to explore how the environment affects female fitness by balancing the costs and benefits of being exposed to males.

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Reproductive interactions with males benefit females by providing access to sperm that is needed for offspring production. However, at a certain point, high male density can also be costly for females. In most species the optimal number of matings is lower for females than males (Arnqvist & Nilsson, 2000). This generates sexual conflict over mating and can lead to male harassment (i.e. repeated unsuccessful mating attempts by coercive males), which, in turn, can generate a wide range of costs for females, including reduced feeding opportunities or increased physical injury and energy expenditure when resisting males (Bateman, Ferguson, & Yetman, 2006; Rönn, Katvala, & Arnqvist, 2006; Takahashi & Watanabe, 2010), often with detrimental effects on female fitness (Crudginton & Siva-Jothy, 2000; Eady, Hamilton, & Lyons, 2007). In consequence, females might sometimes opt to mate simply to decrease harassment (i.e. convenience polyandry; Blyth & Gilburn, 2006; Thornhill & Alcock, 1983). Although there are potential

benefits to mating multiply for females, both direct (e.g. greater male services and resources, Hasson & Stone, 2009; Townsend, Clark, & McGowan, 2010) and indirect (e.g. higher genetic quality offspring or the use of compatible sperm to ensure offspring viability, Jennions & Petrie, 2000; Tregenza & Wedell, 2002), mating can impose direct costs that accumulate with each successive mating (Crudginton & Siva-Jothy, 2000; Fedorka, Zuk, & Mousseau, 2004; Wigby & Chapman, 2005). Consequently, the degree to which females increase their mating rate when more males are present is likely to require that they balance the costs of resisting male mating attempts with the change in net fitness from each successive mating. How the various costs and benefits balance out to influence female fitness is important in driving the evolution of mating systems and reproductive behaviour.

Few studies have tested whether the fitness consequences for females of increased interactions with males vary according to the local environment (Sih, Montiglio, Wey, & Fogarty, 2017; Smith, 2007). This is expected because the environment can influence the relative strength of sexual selection or sexual conflict arising from additional matings and/or resisting more mating attempts. For example, population density might influence the optimal mating strategy of females to acquire direct and indirect benefits

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(Kokko & Rankin, 2006), such that female mating preferences are density dependent (Rosenthal, 2017; Welch, 2003). At low densities of males, females are predicted to be less selective due, in part, to reduced mate availability and the increased time and energy costs of locating mates (Hutchinson & Halupka, 2004; Kokko & Mappes, 2005). Higher male densities will, however, tend to increase the number of male mating attempts. This could lead to either a reduction in female willingness to remate (e.g. Martin & Hosken, 2003) because of the increased costs of excess mating or an increase in female mating rate to lower the short-term rate of harassment (e.g. Rowe, Arnqvist, Sih, & Krupa, 1994).

The environment could also affect the magnitude of the direct benefits that females receive from each mating (e.g. the quantity of beneficial substances transferred in ejaculates, such as nutrients and hormonal triggers that increase egg production; Arnqvist & Nilsson, 2000; Yamane, Goenaga, Rönn, & Arnqvist, 2015). For example, low food availability might decrease male body condition and reduce ejaculate size and composition (Iglesias-Carrasco, Jennions, Zajitschek, & Head, 2018; Perry & Rowe, 2010; Polak et al., 2017) and thereby lower the net benefit of mating for females. Similarly, females in an environment with greater access to food have been shown to remate less often as mating gifts from males are then less valuable (Toft & Albo, 2015). Despite the likely role of the environment in determining the net outcome of female mating decisions, relatively few studies have asked how different environments affect male–female interactions due to the potential for correlated changes in both male harassment and the benefits of additional matings (but see Edvardsson, 2007).

The seed beetle, *Callosobruchus maculatus*, is an ideal model species to investigate the fitness consequences for females of interacting with different numbers of males in different environments. Although females are often polyandrous, the direct benefits of mating multiply are subtle (e.g. males do not provide packaged nuptial gifts such as spermatophores). Previous studies in *C. maculatus* have yielded mixed results that make it difficult to predict the net fitness effect on females of more males being present, owing to the combination of both direct and indirect benefits of additional matings, alongside the cumulative costs of remating. For example, there is evidence that polyandrous females lay more eggs than those mated to a single male (even after controlling for the number of matings; Eady, Wilson, & Jackson, 2000), possibly because of cryptic female choice. Intriguingly, there are also potential direct benefits of mating. Several studies have suggested that fecundity benefits could be attributed to nutrients and water in ejaculates (Eady et al., 2007; Savalli & Fox, 1999; Ursprung, den Hollander, & Gwynne, 2009). As *C. maculatus* is a pest of stored legumes, living in an environment with little or no access to water or food for adult beetles, water is expected to be a limiting resource for females that constrains their reproductive output and life span. Male *C. maculatus* transfer ejaculates that are rich in water (Edvardsson, 2007) so, if male ejaculates are the only water resource available to adult females, we might expect the net benefits of remating to outweigh the costs in dry environments, thereby increasing the mating propensity of females. However, there are other potential costs of mating that could reduce or eliminate the net benefits of polyandry in dry conditions. The costs of copulation in the seed beetle include traumatic wounding of the female's reproductive tract caused by the male's aedeagal spines and the transfer of toxic ejaculatory substances (Crudginton & Siva-Jothy, 2000; Eady et al., 2007; Gay, Eady, Vasudev, Hosken, & Tregenza, 2009). In addition, the presence of more males leads to greater male harassment which can increase the risk of predation and physical damage and reduce the time available for feeding and oviposition, hence shortening female life span (den Hollander & Gwynne, 2009). Surprisingly, despite extensive research in

C. maculatus, we still do not know whether the environment alters the balance between these putative costs and benefits of being exposed to males, and the effect that the variation in the number of males has on female fitness (but see Edvardsson, 2007).

Two previous studies in *C. maculatus* (Edvardsson, 2007; Ursprung et al., 2009) have demonstrated that water availability increases a female's life span and fitness, while reducing her willingness to remate. These findings suggest that water is a limiting resource for females, which might benefit from the water acquired from male ejaculates. Based on these previous findings we predicted that females housed alone in dry conditions would have lower fitness than those in wet conditions. However, we also predicted that females exposed to males would have lower fitness than those housed alone, and that this negative effect would increase with the number of males due to a combination of higher levels of male harassment and the number of mates and/or matings. In the wet environment we expected the costs of being housed with males to be higher than in the dry environment. This is because females can make use of environmental water reducing the advantage of additional matings through the acquisition of water in ejaculates, reducing female willingness to remate and, hence, potentially increasing the level of male harassment and the costs of rejecting males. Therefore, if the costs of increased harassment outweigh the benefits of having access to environmental water and larger ejaculates, we predicted that females housed with males in wet conditions would have lower fitness than those in dry conditions.

METHODS

Study Species

In *C. maculatus*, resources required for adult survival and reproduction are acquired from the host bean during the larval stage (Messina & Slade, 1997). The life cycle begins with females laying an egg on the surface of a host bean. The hatching larva burrows into the bean and remains inside feeding on it for 3–4 weeks until it emerges as an adult.

We used beetles originating from a stock kept at the University of Western Australia since 2005 in cultures of >500 adults breeding on black-eyed beans, *Vigna unguiculata* (Dougherty et al., 2017). This stock was maintained in our laboratory in cultures of >500 beetles at 27 ± 1 °C with a 14:10 h light:dark cycle for three generations prior to our experiment. Stock larvae were raised on black-eyed beans and adults were not provided with food or water.

Ethical Note

This work followed the ASAB/ABS guidelines for the treatment of animals in behavioural research. Information about individuals' housing conditions are described below. Housing conditions, handling and experimental monitoring were all conducted in a way to maximize the animals' welfare. We complied with the Australian regulations for experiments on invertebrates.

Experimental Design

To investigate how the environment (here water availability) influences the costs and benefits for females of being exposed to different numbers of males, we used a 2×3 experimental design where we manipulated water availability (wet or dry) and the number of males (none, one or four) housed with a female after an initial single mating to ensure she had sperm. We had six experimental groups: (1) dry, no male (D0, $N = 49$); (2) wet, no male (W0, $N = 47$); (3) dry, one male (D1, $N = 47$); (4) wet, one male (W1,

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