

The effects of age at mating on female life-history traits in a seed beetle

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Age at first reproduction is an important component of life history across taxa and can ultimately affect fitness. Because genetic interests of males and females over reproductive decisions commonly differ, theory predicts that conflict may arise over the temporal distribution of matings. To determine the potential for such sexual conflict, we studied the direct costs and benefits associated with mating at different times for females, using seed beetles (*Acanthoscelides obtectus*) as a model system. Virgin females were resistant to male mating attempts at a very early age but subsequently reduced their resistance. Although we found no difference in life span or mortality rates between females mated early in life and those mated later, females that mated early in life suffered a 12% reduction in lifetime fecundity. Thus, there are direct costs associated with mating early in life for females. Yet, males mate even with newly hatched females. We suggest that these data indicate a potential for sexual conflict over the timing of first mating and that female resistance to mating, at least in part, may represent a female strategy aimed at delaying mating to a later time in life. *Key words*: age at reproduction, cost of reproduction, female resistance, life history, lifetime reproductive success, longevity, senescence. [*Behav Ecol* 18:551–555 (2007)]

Age at first reproduction has profound effects on fitness (e.g., Stearns 1992; Chilton et al. 1993; Moore PJ and Moore AJ 2001; Torres-Vila et al. 2002; Kruger 2005; Omkar et al. 2006), mating preferences (Moore PJ and Moore AJ 2001) and, potentially, offspring sex ratio (Fauvergue et al. 1998), and it covaries with development time (Miyatake 1997). Delayed mating by virgin females in arthropods is sometimes associated with reduced fecundity or fertility and increased longevity (Moore PJ and Moore AJ 2001; Torres-Vila et al. 2002; but see Omkar et al. 2006). Despite the potentially negative effects of delayed reproduction, virgin females may be very resistant to male mating attempts very early in life, which in many cases may reflect their physiological immaturity (e.g., Markow 2000).

Field studies of long-lived organisms have suggested that costs of early reproduction may outweigh the benefits and thus result in delayed onset of breeding (Weimerskirch 1992; Pyle et al. 1997; Kruger 2005). One recent study showed that early reproduction was associated with reduced fitness in female goshawks (*Accipiter gentilis*) (Kruger 2005). Interestingly, this effect was not related to decreased longevity of birds that started to reproduce earlier, but rather was associated with low reproductive output during the first years of reproduction in early breeders. However, other studies have found a substantial cost of delayed reproduction (e.g., McGraw and Caswell 1996; Oli et al. 2002). Although such long-term studies highlight the importance of the age at first breeding for fitness under natural conditions, the correlational nature of these studies precludes strong conclusions about the causes of the observed patterns (Kruger 2005).

In the seed beetle *Acanthoscelides obtectus*, Parsons and Credland (2003) showed that females produce fewer eggs during the second day after the emergence than later in life and that egg-to-adult survival was lower for the eggs produced

during the second day compared with those produced on the third to seventh days. Early mating may thus be suboptimal for females, and this may be reflected in the resistance behaviors seen in young virgin *A. obtectus* females. In contrast, males should stand to gain from mating with newly matured virgin females in this species in terms of paternity success [mating induces an efficient nonreceptivity to further matings in females; Rugman-Jones (2003)], and this may be true even if early mating causes decreased fecundity or survival in females (Parker 1979; Arnqvist and Rowe 2005). Therefore, although males should attempt mating with recently matured virgin females, it is less clear how timing of mating affects female fitness.

Here, we experimentally (1) assess whether female resistance to mating is age dependent and (2) measure the direct effects of age at first mating on female fecundity and longevity. We show that female resistance to mating declines with female age and that females mated immediately after emergence have reduced early and lifetime fecundity compared with females mated at the peak of their egg-laying ability. We discuss our results in the light of sexual conflict theory and suggest that the conflict between males and females over temporal distribution of matings may contribute to the evolution of female resistance.

MATERIALS AND METHODS

Experimental procedures

Study organism

Bruchid pests of legumes (e.g., *Acanthoscelides obtectus*) are characterized by a worldwide distribution, as a result of ancient human cultivation of and trade with legume seeds (Alvarez et al. 2006), and large populations are often found in seed storages. The laboratory environment represents a good approximation of this “natural” environment (Tucic et al. 1996; Fox et al. 2003; Messina and Karren 2003). *A. obtectus* populations have been known from Europe for more than a century, where they thrive in stored beans (Huignard and Biemont 1981). The population used in this study was obtained by mass-mating beetles from 3 different locations in

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the vicinity of Belgrade (Tucic et al. 1996), and it has been kept under laboratory conditions for more than 150 generations. The population was kept in our laboratory for 8 generations prior to performing the experiments reported here. Thus, the beetles used originate from populations adapted to bean storage conditions, and they have subsequently adapted to the laboratory environment. The rationale behind using populations adapted to the laboratory environment was recently discussed by Rice et al. (2005, 2006), who also coined the term "island laboratory analysis." In short, we suggest that our experiments were conducted in an environment that well reflects the natural conditions for our study population.

This population has been maintained at a large population size (~5000 individuals) (Tucic et al. 1996). We kept the beetles at 28 °C and 65% relative humidity on biodynamically grown white kidney beans, *Phaseolus vulgaris*, that were frozen prior to use. We isolated individual beans showing gray "windows" produced by prepupal larvae in plastic containers. Although Tucic et al. (1991) showed that even extreme differences in larval density (such as 1–2 vs. 10–15 larvae per bean) have no significant effect on female fecundity and longevity, we controlled for potential effects of larval density by selecting only beans with 4–8 prepupal windows. We inspected beans several times per day for newly emerged adults.

Female egg-laying behavior in *A. obtectus* is triggered both by mating and the presence of beans (e.g., Leroi 1981). However, in populations infesting bean storages such as the one used here, females have constant access to beans.

The effect of female age on female mating propensity

We exposed randomly selected virgin females that were 0 ($n = 100$), 24 ($n = 50$), 48 ($n = 41$), 72 ($n = 100$), 96 ($n = 23$), or 120 ($n = 23$) h old to a single 24- to 72-h-old randomly selected virgin male each, in 35-mm Petri dishes, and monitored their behavior for 30 min. Male age was standardized for each experiment (see below). We recorded whether mating occurred, time from the start of the exposure to mating, and copulation duration.

Age at mating and reproductive performance

We enclosed virgin females that were either newly hatched (0 days old; henceforth, females mated early in life; $n = 100$) or 72 h posthatching (3 days old; henceforth, females with delayed mating; $n = 100$) individually with a virgin male for 48 h. Parsons and Credland (2003) used a 24-h exposure period, but preliminary experiments indicated that matings are sometimes not achieved within the first 24 h with newly hatched females. *A. obtectus* are polyandrous yet extremely resistant to remating (Rugman-Jones 2003; Maklakov et al. 2006). We therefore assume that females did not remate during the 48-h exposure period. We had a constant supply of hatching males such that the age of virgin males at the start of the experiment was standardized for both treatments. *A. obtectus* males are protandrous; therefore, we collected males over a period of 48 h and kept them for another 24 h prior to the start of the experiment. A single white kidney bean was placed into the dish to stimulate reproductive maturation in females. After 48 h, we removed the males and transferred the females to another Petri dish with 10 fresh white kidney beans. The dishes were checked daily to record female life span. Hatched and infertile eggs were counted 10 days after female removal in the first dish and 10 days after female death in the second dish. All beetles were weighed prior to mating. Thus, we measured female longevity, early (first 48 h) and total lifetime fecundities, and hatching success for each female. We also estimated the rate of female senescence in both treatments.

Data analysis

We used a contingency table test to analyze the probability of mating at different female ages and Kruskal–Wallis test for the time to mating (SYSTAT 11). Female early and lifetime fecundities, as well as longevity, were modeled in SYSTAT 11 with male and female body masses as covariates. The proportion of unhatched eggs was arcsine square root-transformed prior to analysis. A few females that did not produce any fertile eggs ($n = 8$) were removed prior to analysis and one female escaped. The final sample sizes were $n = 94$ for early mating females, and $n = 97$ for females with delayed mating. Rates of senescence were estimated and analyzed using Win-Modest 1.0.2 (Pletcher 1999).

RESULTS

The effect of female age on female mating propensity and copulation duration

We observed no apparent differences in male persistence, and males in all treatments courted females with similar intensities. Females exhibited a range of resistance behaviors toward courting males, including evasive locomotion and kicking toward courting males with their rear legs. Female age significantly affected the proportion of females that mated ($P < 0.001$, Pearson $\chi^2_5 = 220.91$; Figure 1a) as well as time to mating from the start of the exposure to males ($P < 0.001$, Kruskal–Wallis test: $H = 26$, degrees of freedom [df] = 5; Figure 1b). The proportion of females that mated increased from 0 to 48 h of age and then remained constant, and the time to mating followed a reversed pattern (Figure 1a,b). There was, however, no significant effect of female age at mating on copulation duration ($P = 0.118$, Kruskal–Wallis test: $H = 8.78$, df = 5).

The effect of timing of mating on fecundity and longevity

There was no significant difference in mean life span of females mated early in life (19.29 ± 0.4 days) and those mated late in life (18.74 ± 0.34 days) ($P = 0.3$, $t_{189} = 1.04$). The analysis of age-dependent rates of mortality also did not reveal any significant differences in baseline mortality rate (frailty) ($P = 0.85$, $\chi^2_1 = 0.035$) or in the demographic rate of senescence ($P = 0.072$, $\chi^2_1 = 3.23$). However, when female body mass and early life reproductive investment (i.e., fecundity during the first 48 h) were taken into account in an analysis of covariance, there was a significant effect of treatment on female longevity: the residual life span of females mated early in life was 18.33 ± 0.39 days and that of delayed mating females was 19.67 ± 0.38 days (mating treatment: $P = 0.028$, $F_{1,186} = 4.9$; female body mass: $P < 0.001$, $F_{1,186} = 23.49$; male body mass: $P = 0.46$, $F_{1,186} = 0.54$; early fecundity: $P < 0.001$, $F_{1,186} = 24.19$).

Females with delayed mating produced more eggs, both during the first 48 h after mating (34.22 ± 2.49 eggs vs. 8.8 ± 0.79 eggs; treatment: $P < 0.001$, $F_{1,187} = 104.19$; female body mass: $P < 0.001$, $F_{1,187} = 16.83$; male body mass: $P = 0.6$, $F_{1,187} = 0.28$) (Figure 2) and during their entire life span (79.02 ± 2.22 eggs vs. 71.32 ± 2.04 eggs; treatment: $P < 0.001$, $F_{1,187} = 12.7$; female body mass: $P < 0.001$, $F_{1,187} = 75.96$; male body mass: $P = 0.068$, $F_{1,187} = 3.37$), although early mating females produced more eggs after the initial 48 h than did delayed mating females (62.52 ± 1.74 eggs vs. 44.8 ± 2.18 eggs; treatment: $P < 0.001$, $F_{1,187} = 40.35$; female body mass: $P < 0.001$, $F_{1,187} = 19.08$; male body mass: $P = 0.216$, $F_{1,187} = 1.54$) (Figure 2). There was no significant difference between the treatments in egg hatching rate ($P = 0.449$, $F_{1,187} = 0.575$). Consequently, delayed mating females produced more hatched

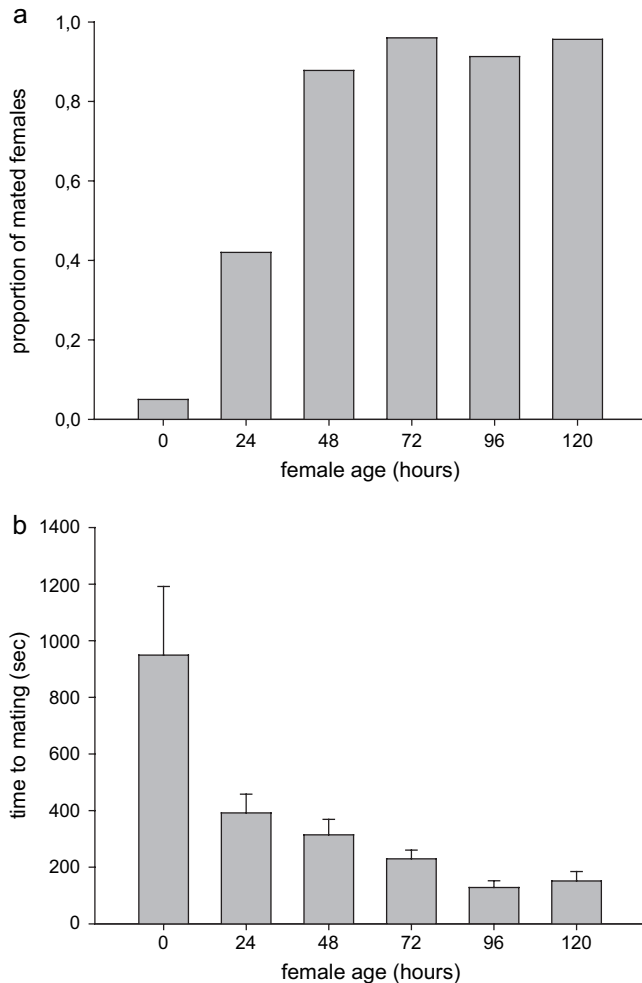


Figure 1
The effect of age (0, 24, 48, 96, and 120 h old) on the mating propensity of virgin females, measured as the proportion of females mated within 30 min (a), and time to mating (\pm SE) from start of exposure to males for those that mated (b).

eggs than did early-mated females during their lifetime (75.12 ± 2.18 hatched eggs vs. 66.4 ± 2.09 hatched eggs; treatment: $P < 0.001$, $F_{1,187} = 14.86$; female body mass: $P < 0.001$, $F_{1,187} = 65.97$; male body mass: $P = 0.042$, $F_{1,187} = 4.21$).

DISCUSSION

Nearly, all females that were exposed to males for 48 h mated and produced fertile eggs, irrespective of age at first mating. Females that were exposed to males immediately after hatching and mated early in life produced very few eggs during the first 48 h compared with females that were exposed to males 72 h after hatching. Although females mated early in life produced more eggs than delayed mating females during the rest of the life span, the total lifetime fecundity was considerably higher when age at first mating was delayed. There was no reduction in the fertility of eggs among delayed mating females. These results show that age at first mating affects female fitness and suggest that early mating is suboptimal for females.

We see 3 factors that might have contributed to the results we observed. First, bruchid males possess spines on their genitalia that damage the female reproductive organs

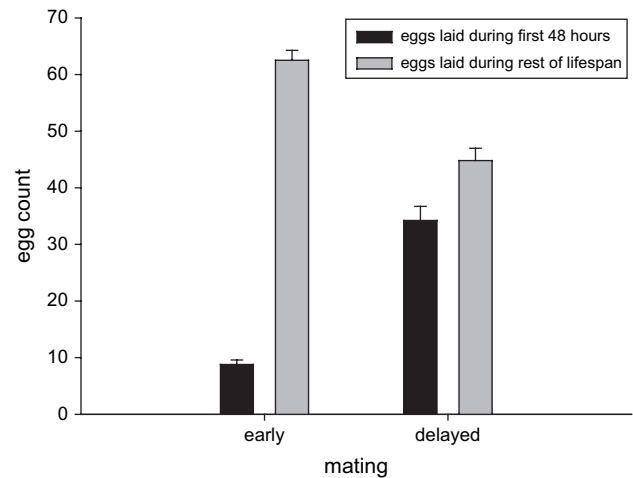


Figure 2
Number of eggs laid by females mating early in life and those with delayed mating during the first 48 h after mating and during the rest of their life span (mean fecundity \pm SE).

(Crudginton and Siva-Jothy 2000). Young females may suffer more harm from this because their internal reproductive organs may not be fully hardened after eclosion. Second, *A. obtectus* males transfer toxic seminal substances to females during copulation (Das et al. 1980). The effect of such toxic compounds on newly hatched females may be more severe if the permeability of their reproductive organs is higher. Third, males also transfer seminal substances that elevate egg production in females (Das et al. 1980). Mating early in life may thus trigger egg production in young females despite their reproductive system not being fully mature, which could result in suboptimal functioning of their reproductive organs.

We also found that the probability of mating among virgin females increased as females aged, and we interpret this as virgin females reducing their resistance to mating as they age. We note that variation in male persistence could, in theory, have contributed to these results. However, we deem this highly unlikely for 2 reasons. First, the fact that copulation duration did not differ across female age suggests that males did not discriminate among females of varying age, given that males have some control over copulation duration (Edvardsson and Canal 2006). Second, and more importantly, male *A. obtectus* are very persistent indeed in their mating attempts and show little or no selectivity: they attempt to mate not only with live females of any age but also with dead females and other males (Maklakov AA, personal observation). Indeed, males invariably tried to mate with females in all our behavioral trials. Moore PJ and Moore AJ (2001) have found that female cockroaches *Nauphoeta cinerea* require less courtship to mate once they passed the optimal mating stage of 6 days, but this reduction in “choosiness” seems to correlate with a reduction in fertility. However, *A. obtectus* females produced more eggs when they mated at the age of 72 h compared with when newly hatched (cf. Omkar et al. 2006), which suggests that higher resistance to mating early in life may reflect direct selection to avoid suboptimal matings imposed by persistent males. In this sense, our results are in line with research on variation in female resistance to mating in water striders, where it has been shown that females adaptively modulate resistance according to direct factors such as female state, ecological conditions, and the rate of male harassment (Rowe et al. 1994; Lauer 1996; Lauer et al. 1996; Arnqvist 1997). We note that there may also be indirect effects of resistance to

mating that may additionally explain the very maintenance of female resistance itself (e.g., Cameron et al. 2003).

We found no significant effect of the age at first mating on female longevity. Reproductive effort early in life is predicted to trade-off with survival late in life (e.g., Stearns 1992). Early mating females started reproducing earlier than delayed mating females but produced very few eggs early in life and less eggs overall, which suggests a lower net reproductive rate compared with delayed mating females. When early reproductive effort was statistically controlled for, delayed mating females had longer residual life span.

The genetic interests of males and females commonly differ, and this fact forms the basis for sexual conflict (Trivers 1972; Parker 1979; Arnqvist and Rowe 2005). Sexual conflict can result in sexually antagonistic coevolution (Parker 1979; Holland and Rice 1998). Such coevolution may affect the evolution of a variety of traits in both sexes and may indirectly shape mating systems and potentially generate speciation (Rice 1996; Parker and Partridge 1998; Arnqvist et al. 2000; Gavrillets 2000; Arnqvist and Rowe 2002, 2005; Chapman et al. 2003; Arnqvist 2004). It is clear that sexual conflict over female mating rates is a consequential form of conflict (Arnqvist and Nilsson 2000), and considerable effort has been invested in assessing the effects of polyandry on male and female fitness. This includes manipulations of female mating rate (e.g., Arnqvist 1989; Chapman and Partridge 1996; Baer and Schmid-Hempel 1999; Eady et al. 2000; Stutt and Siva-Jothy 2001; Arnqvist et al. 2005; Maklakov et al. 2005), artificial selection experiments using monogamous versus polygamous selection regimes (Holland and Rice 1999; Martin and Hosken 2004; Martin et al. 2004), and comparative studies (Wiklund et al. 2001; Arnqvist and Rowe 2002; Wedell et al. 2002). However, sexual conflict over mating is in theory not limited to mating frequency. For example, Holland and Rice (1998) argued that males may induce females to mate suboptimally in terms of frequency, time, or space. In order to demonstrate such sexual conflict over timing of mating, however, one must assess the costs and benefits of mating at different times and show that the optimal timing of mating differs between the sexes.

There are several reasons to believe that mating with newly hatched virgin females is beneficial for males in this species. Mating induces oviposition and causes a dramatic reduction in female receptivity to remating (Rugman-Jones 2003). Moreover, *A. obtectus* exhibit very low remating rates overall (Rugman-Jones 2003 and references therein; Maklakov et al. 2006). Actually, female resistance to remating is so pronounced in this species that some authors regard *A. obtectus* as being monandrous, both in laboratory populations and in nature (Jermy 1970, cited in Rugman-Jones 2003). Experiments on the population used here have shown that *A. obtectus* are, in fact, polyandrous but that only about half of all females remate during the first 11 days of their lives (Maklakov et al. 2006). Thus, males that succeed in mating with a young virgin female will father all eggs produced by this female for, typically, at least a few days. Conversely, a male that refrains from mating with a newly hatched virgin female is unlikely to gain any paternity success with that female as she will likely mate with another male. Precopulatory mate guarding does not occur in this system, females are continually harassed by males, and unmated females are therefore rare at any given time (Rönn et al. 2006). Therefore, mating with newly hatched females should be beneficial to males even if the lifetime fecundity of their mates is reduced by mating early in their life, especially because the costs of mating are likely to be fairly low to males (Huignard and Biemont 1974).

In conclusion, we show that mating very early in life is associated with direct costs for female *A. obtectus* beetles and that resistance to male mating attempts declines with age among

virgin females. Theory predicts that males will evolve to impose matings on immature females even when it reduces female net reproductive success in cases where the reproductive benefits to males are large relative to the costs to males (Parker 1979). Our results suggest that there is a potential for sexual conflict over female age at first mating. Such conflict may be common in natural systems (Markow 2000; Arnqvist and Rowe 2005) and can potentially explain at least part of the variation seen in female resistance to mating. We also suggest that we need more studies across different taxa that assess the direct and indirect fitness consequences of the temporal distribution of mating for females and males (Markow 1985; Omkar et al. 2006).

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