



Costs to females and benefits to males from forced copulations in fruit flies

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Forced copulation, which is perhaps the most extreme form of sexual conflict, is ubiquitous among many species including humans. To better understand the evolution and maintenance of forced copulations, it is imperative to assess their costs and benefits. We followed up on recent studies indicating frequent forced copulations in two wild populations of fruit flies, *Drosophila melanogaster*, and quantified their effects on males and females under controlled laboratory settings. Compared to females that mated consensually, females that were forcibly mated had fewer progeny, higher mortality rates and higher frequencies of wing damage that prevented flight. Males that forcibly copulated fathered much fewer progeny than did males that mated consensually. The reasons for the relatively small reproductive gains to males from forced copulations were the lower female fertility and higher female mortality from forced than consensual copulations as well as the higher frequencies of rematings by females that were forcibly copulated. It is likely that males attempt to force-copulate in spite of the low potential reproductive gain because of the scarcity of sexually receptive females and the consequent low probability of attaining the high fitness associated with consensual matings.

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In most animals, females invest more resources in reproduction than males. This generates divergent mating strategies between the sexes such that males often fight amongst themselves for access to females, females are more selective than males in choosing mates, and males may harm females or coerce them to mate (Darwin 1871; Trivers 1972; Parker 1979; Arnqvist & Rowe 2005). The last strategy constitutes conflict between the sexes, which can lead to an evolutionary arms race where males evolve better armament and females evolve improved defences (Parker 1979; Clutton-Brock & Parker 1995; Arnqvist & Rowe 2005).

There have been excellent research programmes devoted to studying particular types of sexual conflict and their evolutionary consequences (e.g. Arnqvist & Rowe 1995; Rice 1996; Rice et al. 2006; Arnqvist & Tuda 2010; Rowe & Arnqvist 2012). Surprisingly, however, one of the most extreme manifestations of sexual conflict, forced copulation, has received relatively little attention in spite of its prevalence among many animals, including humans (Thornhill 1980; McKinney et al. 1983; Smuts & Smuts 1993; Thornhill & Palmer 2000). Importantly, to understand the evolutionary dynamics resulting from forced copulation, we need to quantify how its exact costs and benefits translate into male and female reproductive success. As far as we know, no study has quantified

reproductive benefits from forced copulations in males. In females, we know of only a single study by Thornhill (1984), in which female scorpion flies (*Panorpa latipennis*) provided with nuptial gifts in consensual matings laid more eggs than females that were forcibly copulated with males offering no nuptial gifts.

Seeley & Dukas (2011) substantiated Markow's (2000) observations of forced copulations in field populations of *Drosophila melanogaster* and *Drosophila simulans* in Arizona by recording forced copulations in a wild Canadian population of *D. melanogaster* as well as in laboratory stocks of Canton-S *D. melanogaster*. Mature males in both populations intensely courted newly eclosed, teneral females, identified by their soft, pale bodies and folded wings. The males attempted to mount these females and succeeded in copulating in about 20% of the trials. The females fought off the males' copulation attempts and continued walking and kicking during copulations. The teneral females had about 10 times longer mating latencies and approximately 25% shorter mating durations compared to sexually mature females, most likely owing to the teneral females' persistent struggles. Limited data indicated that forced copulations resulted in fewer offspring than consensual matings (Seeley & Dukas 2011). Forced copulations also seemed to cause more physical damage and higher mortality rates than consensual matings (C. Seeley & R. Dukas, unpublished data).

The data from forced copulations in fruit flies open up promising opportunities for thorough examinations of the fitness consequences as well as neurogenetic mechanisms involved in this extreme type of sexual conflict. Here, we focus on the former. We conducted a series of experiments to quantify the relative outcomes

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from forced versus consensual matings in both males and females. Specifically, our core predictions regarding females were that, compared to females that mate consensually when mature, females forced to copulate when teneral would have fewer progeny and incur higher frequencies of wing damage and premature death. Our main prediction regarding males was that males that forcibly mate with teneral females would sire fewer progeny than males that consensually mate with mature females.

GENERAL METHODS

We used two lines of fruit flies (*D. melanogaster*) kept under standard conditions in population cages containing a few thousands flies (Seeley & Dukas 2011). The wild type was Canton-S and the marker flies were of the sepia stock, which has been previously used for identifying paternity because the recessive eye-colour mutation does not affect behaviour and fitness (Gromko et al. 1984b; Bretman et al. 2009). We collected teneral females using an aspirator within a few minutes post eclosion. To collect males, we anaesthetized flies with CO₂ 8 h after eclosion and placed males in groups of 20 per regular food vials. We transferred males individually into vials 1 day before each test as this results in higher levels of male sexual activity (R. Dukas, unpublished data). Observers blind to female treatment recorded all the data. The statistical analyses involved ANOVAs on either the raw data when they met ANOVA assumptions or log-transformed numbers, which met ANOVA assumptions after transformations. We used nonparametric tests in cases where transformations failed to normalize the data.

We conducted four experiments, two focusing on the females and two on the males. The two experiments for each sex varied slightly in focus and protocol as detailed below.

FEMALE EXPERIMENT 1

Here we wished to examine costs to females from experiencing male coercion. We used only Canton-S flies in this experiment. Females interacted with either mature females or mature males when teneral and then had the opportunity to mate/remate when sexually mature 2 days later. We had four female treatments that differed in their experience: (1) females that were forcibly mated when teneral on day 1 and did not remate when sexually mature on day 3, (2) females that were forcibly mated when teneral and remated on day 3, (3) females that were placed with males and experienced only courtship and copulation attempts when teneral on day 1 and then mated consensually when sexually mature on day 3, and (4) females that were placed with females when teneral on day 1 and then mated consensually when sexually mature on day 3.

We predicted fewer progeny and higher frequencies of wing damage and premature mortality in females that were forcibly mated when teneral (treatments 1 and 2) than in females that consensually mated when sexually mature (treatments 3 and 4). We further expected that forcibly mated teneral females that did not remate when sexually mature would produce fewer progeny than those that did remate when sexually mature (treatments 1 versus 2, respectively), and that females that mated for the first time when sexually mature would produce fewer progeny when they had been exposed to males rather than females when teneral (treatments 3 versus 4, respectively).

Methods

On day 1, we collected teneral females and placed each in a regular 40 ml vial with two 4-day-old males. We also placed

20 teneral females each in a regular 40 ml vial with two 4-day-old females. We recorded all matings lasting at least 2 min. We set up 168 vials with teneral females and males and recorded matings in 34% of the vials. The average (and range) of forced-mating latency and duration were 30 min (3–71 min) and 698 s (150–1200 s), respectively. Either at the end of mating, or once 2 h had elapsed, we transferred the teneral females into regular food vials with a sprinkle of live yeast and placed them in an environmental chamber. On day 3, we transferred each of the now sexually mature females into a vial containing a 4-day-old male and recorded matings for 1 h. As expected, the frequency of matings of females that were forcibly mated when teneral were much lower than those of the virgin females (28%, $N = 53$, versus 100%, $N = 39$; $\chi^2_1 = 47.6$, $P < 0.001$). Either at the end of mating or once 1 h had elapsed, we transferred the females into regular food vials with a sprinkle of live yeast, recorded their wing damage and placed them in an environmental chamber. We transferred the females into fresh food vials daily and recorded mortality. We kept transferring females into fresh food vials as necessary until they either died or ceased laying fertile eggs, and later counted all adult progeny. Our data set included 96 females.

Wing damage and longevity

Wing damage consisted of part of the wing not extended fully, with a few veins fused together. Flight tests inside cages indicated that females with wing damage had limited or no flight capabilities. Instead, they either walked or hopped. The wing damage analysis included only the 92 females still alive at the time of data recording on day 3. Because most females (91%) survived longer than their sperm stores, we report the proportion of females that died prematurely, defined as death before day 10. We conducted the longevity statistics on the whole data set using Kaplan–Meier survival analyses.

Results

Progeny

The number of progeny varied significantly between female treatments (ANOVA: $F_{3,92} = 7.8$, $P < 0.001$; Fig. 1a). Females that were forcibly mated when teneral had significantly fewer progeny than females consensually mated when sexually mature ($t_{92} = 4$, $P < 0.001$). Note that this difference was not caused by infertility because only 8% and 5% of the females forcibly and consensually mated, respectively, had zero progeny ($\chi^2_1 = 0.3$, $P = 0.7$). Our two additional comparisons, however, revealed no significant differences in the number of progeny between either the females that were forcibly mated when teneral that remated on day 3 and the females that were forcibly mated when teneral that did not remate on day 3 ($t_{92} = 1.15$, $P = 0.25$), or between the females consensually mated when mature that were either exposed to males or females when teneral ($t_{92} = -0.5$, $P = 0.6$; Fig. 1a). An analysis including only the females that lived through the end of the experiment revealed a similar pattern of fewer progeny in females that were forcibly mated when teneral than in females that consensually mated when sexually mature ($t_{83} = 3.4$, $P < 0.001$). That is, the dominant contributor to overall progeny was female fertility rather than premature mortality.

Wing damage and mortality

More forcibly mated females suffered wing damage ($\chi^2_1 = 13.1$, $P < 0.001$) and mortality (Kaplan–Meier: $\chi^2_1 = 3.7$, $P = 0.054$) than females exposed to either males or females when teneral and consensually mated when mature (Fig. 2a). A further analysis comparing the females forcibly mated when teneral versus the females exposed to males but not forcibly mated when teneral

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