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Benefit of polyandry in a highly monandrous species when females mate with already mated males

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Abstract Female mating frequency varies among animal taxa. A benefit to females of remating has usually been found, but almost all tests have been with polyandrous species. A species being monandrous does not guarantee that mating only once benefits the female, instead the monandry may result from sexual conflict, where her failure to remate benefits her mate, but not her. **The parasitoid wasp *Spalangia endius* (Hymenoptera: Pteromalidae) is highly monandrous. Females do not benefit from either immediate or delayed remating when their first mate is virgin. However, some females are likely to mate with already mated males because sex ratios are female-biased.** Here the effect of experimentally-induced polyandry on female fitness was examined for females whose first mate had already mated four times, i.e., for fifth females. **Fifth female *S. endius* produce significantly fewer daughters than first females.** Production of daughters, but not sons, requires sperm in hymenopterans. **Fifth females were experimentally induced to mate with a second male, by preventing such females' first mate from providing postcopulatory courtship. The proportion of female offspring produced by these polyandrous fifth females was greater than by monandrous fifth females and not significantly different than by monandrous first females. Total number of offspring did not differ among the three treatments.** These results show that **there are conditions under which females benefit from polyandry in this highly monandrous species and that the benefit is through effects on offspring sex ratio, not fecundity.**

Key words Monandry; Remating; Polyandry; Mating history; Sex ratio; Sexual conflict

Significance statement
Mating frequency varies widely among animals. In most of the more than one hundred past studies of insect species in which females mate multiply, females benefit from remating. However, this same question has been addressed in few species in which females mate just once. In the tiny parasitic wasp studied here, females were tricked into remating. Females benefited from remating if their first mate had previously mated multiple times. The benefit was not producing more offspring, but rather being able to produce a greater proportion of daughters. Sons can be produced without sperm in wasps and wasp relatives. Explanations for why females do not normally remate include that they have been manipulated by their first mate and that waiting for a male means sacrificing searching for hosts.

Introduction

Animals vary widely in their number of mating partners (Krasnec et al. 2012). Given the opportunity, males are usually polygynous, rarely monogynous (Schneider and Fromhage 2010). In contrast, there are many species in which females mate once (monandry) and many in which females mate multiply (polyandry) (Taylor et al. 2014). Among insects, monandry is less common than polyandry (Ridley 1988), and the adaptiveness of monandry remains poorly understood (Arnqvist and Nilsson 2000; Monceau and van Baaren 2012). Monandry may benefit a female and/or for her first mate, but overcoming monandry may benefit her subsequent suitors (Arnqvist and Rowe 2005).

Most experimental tests of the effects of mating frequency on female fitness have been with polyandrous species (Ridley 1988; Arnqvist and Nilsson 2000; Okada et al. 2017). A meta-analysis of 122 studies shows a fecundity increase from multiple mating, even in species without nuptial feeding, although mating too many times decreases fitness (Arnqvist and Nilsson 2000). No hymenopterans were included.

Hymenopterans are of special interest because, in many, sperm are necessary for the production of daughters; sperm are not necessary for the production of sons. Thus, even unmated females can produce sons. Whether unmated females produce as many total offspring as mated females varies among species (e.g., Sousa and Spence 2000; King 2002a; Cheng et al. 2004 and references therein; Metzger et al. 2008). Offspring sex ratios of parasitoid wasps tend to be female-biased (Heimpel and Lundgren 2000), which appears to be adaptive, e.g., as described by local mate competition theory (Hamilton 1967; Hardy 1994; King 2002b). If a female fails to mate often enough or mates with male(s) with insufficient sperm, she may be constrained to produce a sex ratio that is more male-biased than is optimal (Charnov 1982; Steiner and Ruther 2009; West 2009; Boulton et al. 2015).

In the present study, the fitness consequence of experimentally-induced polyandry was examined in *Spalangia endius*, a parasitic hymenopteran that is highly-monandrous. Less than 5% of females copulate with a second male (King et al. 2005). Females not only avoid remating immediately after mating is complete, but also after a dramatic drop in daughter production after 4 d of oviposition (King and Bressac 2010). Sex ratios of *S. endius* appear to be adaptive in conformance with local mate competition theory (King 2002b).

Fitness of females that mate once versus multiply has been examined in only a few highly monandrous insects (Baer and Schmid-Hempel 2005; Arnqvist and Andres 2006; King and Bressac 2010; Jiao et al. 2011). If females of monandrous species benefit from multiple mating like polyandrous species do (Arnqvist and Nilsson 2000), this would suggest that monandry may have evolved because males benefit more by preventing their mates from remating than females do from multiple mating and than males do from mating already mated females.

The few studies that have examined how a female's fitness is affected by being monandrous versus polyandrous have done so by experimentally manipulating females to remate. Artificial insemination with sperm from more than one male has a negative effect on queen fitness in the bumble bee *Bombus terrestris* (Baer and Schmid-Hempel 2005). Remating has no detectable effect on female fitness in *S. endius*, in the house fly or in a wolf spider, at least when the males are virgin (King and Bressac 2010; Arnqvist and Andres 2006; Jiao et al. 2011). However, polyandry seems most likely to be beneficial when a female's first mate is sperm-depleted. Thus, the present study of *S. endius* tested whether a female benefits from remating when her first mate has already mated multiple times.

Some *S. endius* females are likely to mate with already-mated males because there are more females than males (King and Fischer 2010). Female *S. endius* whose mate already mated four times previously, i.e., fifth females, produce the same number of total offspring but fewer daughters than first females do. The present study tests whether such females benefit from remating, either through greater offspring production or through more female-biased sex ratios, and how any benefit compares to having mated with a virgin male initially.

Methods
Biology of *Spalangia endius*
Spalangia endius develops within fly pupae that live amongst decaying organic matter (Rueda and Axtell 1985b). Hosts occur singly or in multiples, and generally one *S. endius* emerges per host; two offspring are produced per host only about 3% of the time (Broski and King 2017). Males begin emerging before females and wait multiple days for females to emerge from nearby hosts (King 2006). After mating, females sometimes have to disperse in order to find fresh hosts, and sometimes fresh hosts will be available nearby (King, personal observation). A *Spalangia* male emerges from his host with his lifetime supply of sperm (Gerling and Legner 1968; King and King 1994). Males provide no nuptial gifts or parental care (King 2002a).

Mated females release an antiaphrodisiac when approached (Mowles et al. 2013), with the result that females that have already mated tend not to be mounted. In addition, if mounted, mated females rarely open their genital orifice (King et al. 2005; King and Fischer 2010). Opening is necessary for copulation. Failure to open appears to result from some aspect of postcopulatory courtship (King and Fischer 2005). Females can be manipulated into a second mating by preventing the first male from providing postcopulatory courtship (King and Bressac 2010). Females that have not received postcopulatory courtship are still attractive and receptive to subsequent males (King and Fischer 2005).

Production of *Spalangia endius*
The *S. endius* was a strain originally collected from Zephyr Hills, Florida, U.S.A. They were reared at approximately 25°C with a photoperiod of 12 h light: 12 h dark. The host *Musca domestica* was reared so as to produce uniform size host pupae, thereby minimizing variation in body size of the *S. endius* developing in them (King et al. 2014). Parasitized host pupae were individually isolated in glass test tubes (12 x 75 mm) to obtain male and female *S. endius* that were virgin and newly emerged (1-d-old or less). Matings were observed. Each mating was in a clean container, a plastic dish (35 mm diameter x 10 mm height) that was about two-thirds full of dampened sand to keep humidity high, which reduces static.

Effects of remating
I tested whether remating by fifth females allowed them to produce a greater proportion of daughters than not remating and whether remating allowed them to produce as many or more daughters as if they had mated with a virgin male initially. Fifth females were used to match a previous study of the same parasitoid species and to be within the range of how many times a male is likely to mate in nature (King and Fischer 2010). There were three treatments (*N* = 16 per treatment): monandrous fifth females, polyandrous fifth females and monandrous first females.

1) In the monandrous first treatment, females were each presented with a single virgin male, and mating was observed.

2) In the monandrous fifth treatment, females were each presented with a male that had already mated with four other virgin females, and mating was observed.

3) In the polyandrous fifth treatment, females were each presented with a male that had already mated with four other virgin females, and mating was observed. However, this mating was interrupted: the male was removed immediately after he withdrew his aedeagus from the female, i.e., just before postcopulatory courtship would normally begin. Then the female was presented with a second male, this time a virgin male, and the second mating was allowed to complete naturally.

About 10 min after the last mating, each female was presented daily for 7 d with 20 hosts and with honey ad libitum, a total of 140 hosts per female. This is less than the mean of about 80 offspring (maximum of about 120) that a female produced in her lifetime in a previous experiment (unpublished analysis of first experiment in King and Bressac 2010). King (2002a) reported that no female produced offspring from all 20 hosts in a day.

The hosts had pupated within the last 2 d when they were presented to females. One week of hosts was chosen as being sufficient to show meaningful effects on daughter production if they exist. Offspring sex ratio

in the first 7 d of oviposition differs significantly between fifth females and first females, with fifth females producing more sons and fewer daughters (unpublished analysis of King and Fischer 2010). Offspring production drops dramatically within the first week for both types of females, as a result of a drop in daughter production (King and Bressac 2010; King and Fischer 2010). Adult offspring were allowed to complete development, emerge from their hosts, and die. Then because some adults crawl back into a host, the hosts were dissected, and the number of adult sons and the number of adult daughters were counted. The person counting the wasps was blind to what the treatments were.

Statistical analyses

Analyses were with SPSS (IBM Corp 2016). Total number of sons and total number of daughters were each summed across all 7 d for each mother. From those, total offspring production and the proportion of daughters were calculated for each mother. Residuals of a one-way ANOVA (analysis of variance) on offspring production were highly kurtotic and skewed as assessed by a Shapiro-Wilk test; the same was true for the proportion of daughters. Thus, Krukal-Wallis tests, which are nonparametric, were used instead. Post hoc pairwise comparisons of treatments were by an ANOVA when residuals were normally distributed, and by a Mann-Whitney U test otherwise. Conclusions would have been unaffected if a Bonferroni correction had been applied to control for multiple comparisons (Rice 1989).

Results

The number of offspring produced per day in the present study was 0 to 25, and the lifetime number was 11-123. There was no significant effect of treatment on offspring production (Fig. 1; Kruskal-Wallis $X^2 = 3.82$, df = 2, P = 0.15), but there was an effect of treatment on sex ratio (Fig. 2; Kruskal-Wallis $X^2 = 12.20$, df = 2, P = 0.002). Sex ratio did not differ between monandrous first females and polyandrous fifth females (F = 0.35, df = 1, 30, P = 0.56), but the proportion of daughters produced by those two treatments combined was more female-biased than that of monandrous fifth females (Mann-Whitney U = 98.0, n = 32, n = 16, P = 0.001). How
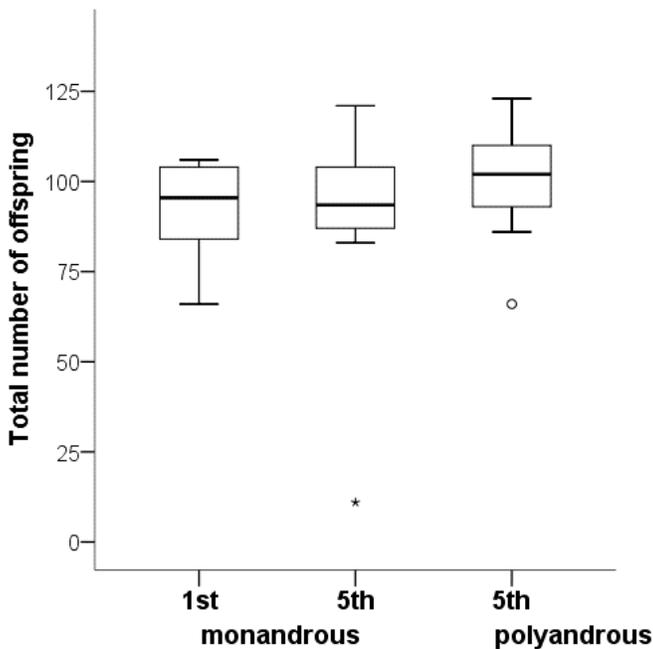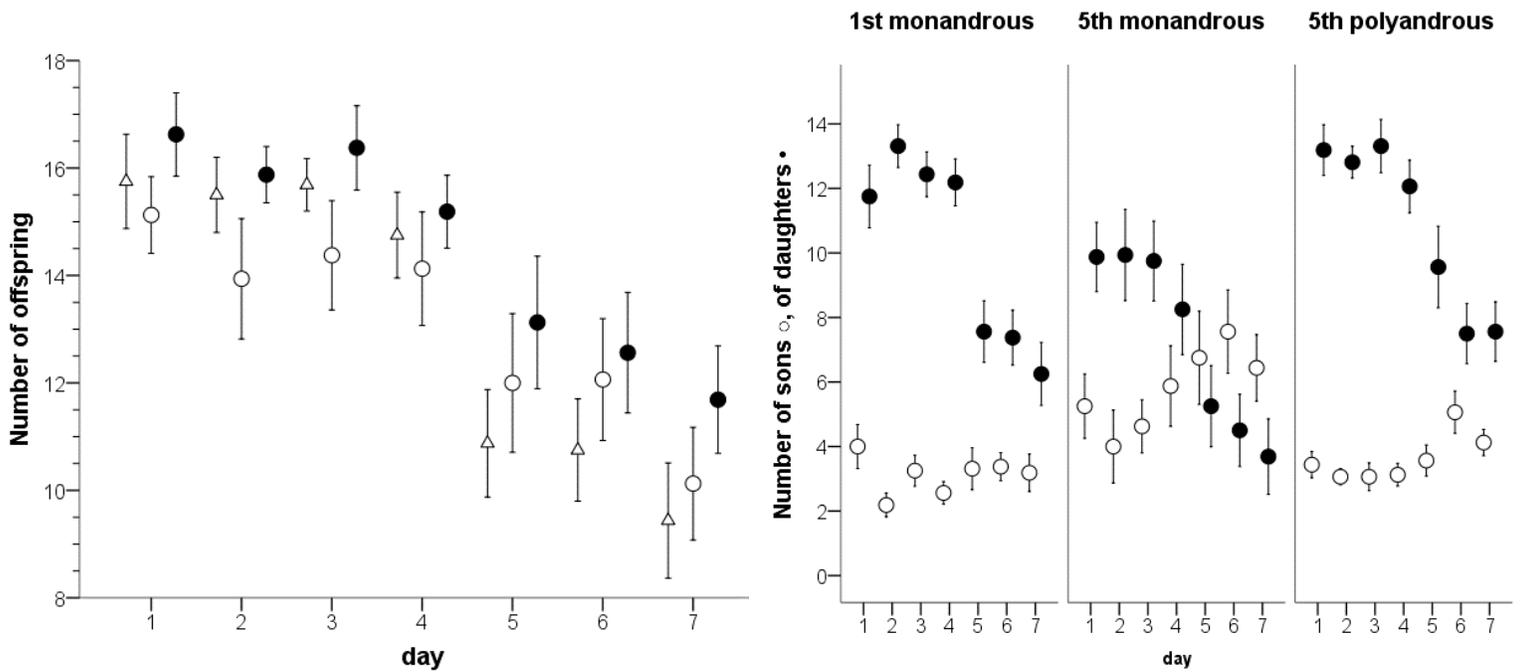

Fig. 1 Total number of offspring added across all 7 d of oviposition for first monandrous, fifth monandrous, and fifth polyandrous mothers
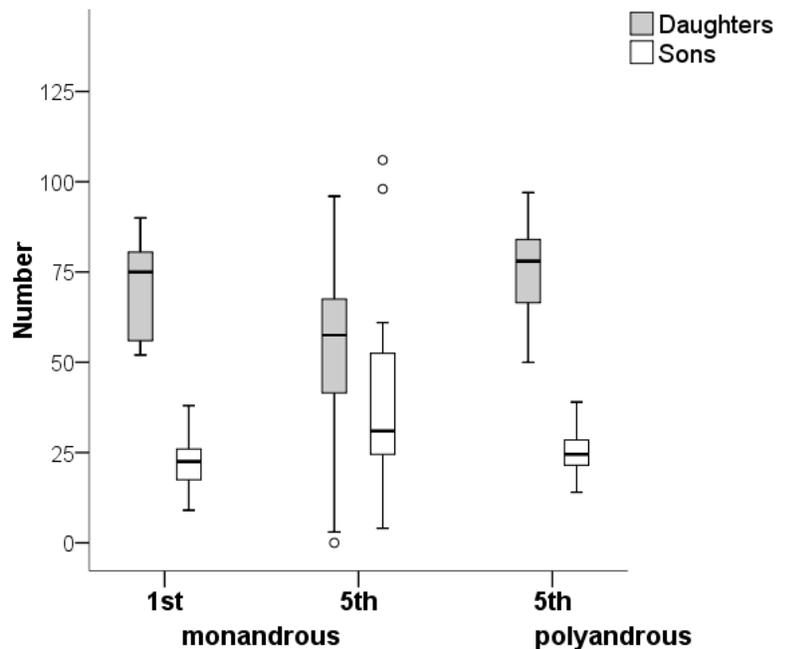
Fig. 2 Total number of sons (○) and total number of daughters (●) added across all 7 d of oviposition

for first monandrous, fifth monandrous, and fifth   polyandrous mothers
 offspring production and sex ratio changed over time in each treatment is shown in Fig. 3 and 4, respectively.

Fig. 3 Total number of offspring among first monandrous (Δ), fifth monandrous (○), and fifth polyandrous (●) mothers during each of 7 d of oviposition

Fig. 4 Number of sons (○) and number of daughters (●) among first monandrous, fifth monandrous, and fifth polyandrous mothers during each of 7 d of oviposition

Discussion

Unlike the lack of a benefit to polyandry when *S. endius* females have first mated with a virgin male (King and Bressac 2010), polyandry was beneficial for females that had mated with a male that had previously mated multiple times. By remating, fifth females increased their proportion of daughters so much that their offspring sex ratios became as female-biased as those of females that had mated only once but with a virgin male (Fig. 2, 4). These results are consistent with previous suggestions that the cost of monandry and benefit of polyandry is most likely to be in females whose first mate has mated multiply before her (Jones 2001; Montrose et al. 2004). In contrast to the effects of remating on sex ratio, but as expected, offspring production was not significantly affected by female mating status, specifically, by whether a female was a monandrous first female, a monandrous fifth female, or a polyandrous fifth female (Fig. 1, 3).

Given the apparent advantage to a female from remating, three non-mutually exclusive hypotheses may explain why *S. endius* females do not normally remate. One explanation is that remating would reduce offspring production by interfering with females beginning to burrow in search of hosts (Rueda and Axtell 1985a; Geden 2002). To remate, a female would have to instead stay on the surface, because that is where males are (King 2002a).

A second explanation is interparty conflict and cooperation. Whether a female remates can be influenced by the behavior of at least three parties: the female, her first mate, and subsequent suitors (Chapman et al. 2003; King and Bressac 2010). The three parties' fitness-interests may or may not all coincide (Parker 1979; Arnqvist and Rowe 2005). The present study suggests that, provided the female's first mate has recently mated multiply, she will benefit from remating, through more daughters allowing her to produce adaptive sex ratios (Hamilton 1967; King 2002b). How the fitness of her first and second mate is affected will depend on patterns of sperm usage in this species. The pattern of sperm precedence is context-dependent in confamilials of *S. endius* (van den Assem and Feuth-DeBruijn 1977; Khanh et al. 2005) and is unknown in *S. endius*. The second *S. endius* mate's expected benefit in our experiment was likely at least as great as the difference in the number of daughters that fifth polyandrous females produce minus the number of daughters that fifth monandrous females produce. That females do not typically remate may indicate that during the species' recent evolutionary history, the benefits of remating to the female and to her subsequent suitors have not exceeded the benefit of monandry to the first male.

A third explanation is that the frequency at which females encounter and mate with males that have already mated four times may be low. Given the sex ratio in this species, males are expected to mate one and a half to three times on average (King and Fischer 2010), and reproductive success is highly variable among males even in the laboratory (King and Napoleon 2006). Thus, some males will have more success than average. The risk of mating with a multiply-mated male will be lower in *S. endius* when virgin males are also present. This is because virgin males are quicker than mated males to approach females, with the result that females usually mate with virgin males when they are present (King and Fischer 2010).

The lack of increased fecundity from multiple mating in the present study of *S. endius* is consistent with the other studies of highly-monandrous species (Baer and Schmid-Hempel 2005; Arnqvist and Andres 2006; Jiao et al. 2011), including King and Bressac's (2010) study of *S. endius*, which used only virgin male. In contrast, in *S. endius,* a sex ratio benefit from remating is seen only when a female's first mate has mated multiply (the present study), not when he is virgin (King and Bressac 2010).

The number of polyandrous parasitoid wasps that have been studied is small, but most do not show a fecundity benefit from multiple mating (Chevrier and Bressac 2002; Cheng et al. 2004; Jacob and Boivin 2005; Khanh et al. 2005; but see mixed results in Boulton and Shuker 2015). This contrasts with a fecundity benefit from moderate multiple mating by females in many other animals, even species without nuptial feeding (Arnqvist and Nilsson 2000). So far, only one of five polyandrous parasitoid wasps show a sex ratio benefit from multiple mating (Chevrier and Bressac 2002; but see Cheng et al. 2004; Jacob and Boivin 2005; Khanh et al. 2005; Boulton and Shuker 2015). The two species where longevity effects have been examined show a positive effect in some conditions (Jacob and Boivin 2005; Boulton and Shuker 2015). There is not yet evidence

of indirect genetic benefits in parasitoid wasps (Boulton and Shuker 2015), but indirect benefits have been seen in some other animals (Slayter et al. 2011). It is important to keep in mind that effects of a given mating system on fitness may not be the same as when that mating system first evolved or first re-evolved in a population. This is because when mating frequency changes, male and female reproductive traits evolve (Katvala et al. 2008; Kraaijeveld et al. 2009). Some of these traits could in turn affect the current benefit of different mating frequencies, e.g., sperm storage, male ejaculation quality and quantity, and timing of dispersal or timing of the switch from attraction to sex pheromones to attraction to host pheromones.

To better understand the evolution of female mating frequency, more studies of highly monandrous species are needed, including tests of effects of indirect benefits. Together, the two studies of effects of multiple mating on female fitness in *S. endius* demonstrate the importance of examining fitness effects on sex ratio, not just fecundity, and demonstrate the importance of examining effects when males have already mated, not just when they are virgin (the present study; King and Bressac 2010).

Compliance with ethical standards

Ethical approval All procedures were in accordance with the ethical standards of the institution at which the studies were conducted

Conflict of interest The author declares no conflict of interest.

Informed consent Informed consent was not required as no human participants were involved.

Data availability The data generated and analyzed during the current study are available in the Harvard Dataverse repository, King BH, 2017, "KingBH_FL_Spalangia_endius_1stf_5thf_5th&1stf.xlsx", doi:10.7910/DVN/NL1EM3, Harvard Dataverse, V1, UNF:6:URbK01VzI+rrr1T/IGxZuA==

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