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Mate choice in males with one-shot genitalia: limited importance of female fecundity

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Male mate choice is expected in species in which future mating opportunities of males are strongly diminished after their first copulation and mate quality is variable unless the costs of choice exceed the benefits. Males of the spider *Argiope bruennichi* are mostly monogynous; they damage their paired one-shot genitalia during copulation and fall victim to sexual cannibalism. Even males that are not cannibalized can achieve a maximum of two matings. Such a high mating effort implies that a male's reproductive success can be increased by selecting the best possible mate. Mate quality may depend on female mating status and/or fecundity. Males should be selected to prefer virgin females over mated ones since previously used female genital ducts can be blocked by genital mating plugs. Fecundity is a common approximation of female quality and in invertebrates is generally correlated with body size and mass. *Argiope bruennichi* females vary in body size and fecundity, providing a basis for male selectivity. By creating binary choice situations in field and laboratory experiments in which search costs were largely removed, we tested whether males show mate choice. There was weak evidence for a male preference based on female phenotype. However, virgin females were significantly preferred over mated females even if the virgin had a less fecund phenotype. We conclude that selective benefits of mating first with a female override potential benefits of choice based on female fecundity, leading to competition for virgin females.

Sexual selection through mate choice is recognized as a major evolutionary force and whether mate choice evolves depends on the balance between the benefits of choice and its costs (Andersson 1994). The magnitude of benefits largely depends on the variation in quality among individuals of the selected sex, while costs are largely influenced by the searching and sampling efforts of the selecting sex (Wiegmann et al. 1999). These costs are largest in sequential choice situations where potential mates have to be located, evaluated and perhaps revisited depending on the sampling rule (Janetos 1980; Janetos & Cole 1981). Sequential choice requires cognitive abilities, involves physiological costs related to sampling and decision making, and is associated with manifold risks of mate search and sampling (Real 1990, 1991; Wiegmann et al. 1996). In addition to the risks of predation, the searching sex may face a certain probability of not finding another, better mate if the first one is rejected or of not finding another partner at all. Hence, in species with sequential mate choice, fitness benefits of choice should be particularly high to balance the costs.

Sequential choice is rarely an issue for the male sex which is generally viewed as facing few limits to mating frequencies (Bateman 1948; Wong et al. 2004). In the absence of paternal care, males are expected simply to mate with every female they encounter, unless the expected encounter rates exceed the available sperm supplies required to fertilize all eggs from multiple females (Trivers 1987). However, in monogynous species males are selected to mate with one or at the most two females (Andrade & Kasumovic 2005; Fromhage et al. 2005, 2008). In spiders with sedentary females and roving males, monogyny has evolved several times independently (Miller 2007). Males generally stop building a web as adults and instead search for mates guided by pheromones that receptive females emit (Foelix 1996; Gaskett 2007). Monogynous males invest maximally in fertilizing a single female, a strategy associated with male sacrifice, sexual cannibalism and genital mutilation (Elgar & Schneider 2004; Miller 2007). Males that invest maximally in a single female can optimize their reproductive success by directing this major investment towards a female of an advantageous mating status and/or of high fecundity (Andrade & Kasumovic 2005). Several studies have found that males of various spider taxa clearly prefer virgin over mated

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females (Gaskett et al. 2004; Andrade & Kasumovic 2005). This preference is highly adaptive in species with a strong first-male advantage that is implemented by female genital morphology or by the application of a mating plug, which can consist of a secretion or broken-off male genitals (Uhl et al. 2010). Female fecundity in most invertebrates, including spiders, is a direct function of female body size at maturation and their subsequent foraging success (Marshall & Gittleman 1994; Head 1995; Uhl et al. 2005). Hence, males are expected to evaluate and select a female partner based on her body size (Bonduriansky 2001). Spiders have been shown to possess the cognitive abilities needed to assess partner quality and behave accordingly, and male mate choice has been demonstrated in a number of species (Huber 2005; Prenter et al. 2006). However, even though male mate choice may be most expected in monogynous spiders, whether males show a preference for large, fecund females has not been experimentally investigated. In a demographic study, males of the monogynous spider *Nephila plumipes* were found in higher numbers on the webs of large females, suggesting that large and fecund females attract more males (Vincent & Lailvaux 2006). Differential attraction may result from signals or cues that can be perceived by the male at different levels: at a longer distance through differences in volatile pheromones or during contact with the web or female's body surface by means of contact pheromones, tactile or vibratory signals (Uhl & Elias, in press). While there is behavioural support for the latter, volatile signals are generally perceived as signalling only the presence or absence of a mating partner. The potential for pheromones to be employed in mate assessment, however, has been underestimated and is mediated by differences in the pheromonal blends (reviewed in Johansson & Jones 2007). In spiders, the first case of mate assessment was recently demonstrated for the spitting spider *Scytodes*: females that showed a preference for males on the basis of their dragline-borne odour produced more and larger eggs after mating with preferred males than with nonpreferred males (Koh et al. 2009). To assess at which level mate choice (here male mate choice) occurs, observations of male behaviour during approach and courtship until copulation are required.

Here we experimentally investigated male mate choice in a sexually cannibalistic species with mostly monogynous males, the orb-web spider *Argiope bruennichi*. Male choice appears likely in this model species for several reasons. First, the species is highly seasonal, all females mature within a short period of time and it occurs at high densities (Schneider et al. 2006). Second, webs of females are often clumped and several webs can occur within a square metre. Third, choice confers fitness benefits for males. There is a first-male advantage in *A. bruennichi* since males leave parts of their sperm transfer organs inside the insemination ducts of the females. These plugs strongly reduce the copulation duration of subsequent males (Nessler et al. 2007; Schneider & Lesmono 2009). However, females possess two insemination ducts and most males (70–80%) are limited to a single insemination because of sexual cannibalism, thereby plugging only one of the two spermathecae of a female (Schneider et al. 2006; Nessler et al. 2007). Mated females are therefore mostly 'one-sided virgins' after their first mating. If a subsequent male uses the virgin side, his paternity success is 48% whereas if he uses the previously used side, his paternity success is 17% (Schneider & Lesmono 2009). At least a coarse distinction between virgin and mated females is possible in *A. bruennichi* since only virgin females emit a volatile substance that attracts males in the field (Chinta et al. 2010). Whether males perceive more detailed information on female fecundity on this level or a subsequent level during courtship remains to be investigated. Females of *A. bruennichi* can vary in body size at maturation with a coefficient of variation of 30%, and clutch size varies by a similar magnitude (37% in the first clutch); female adult size and clutch size are correlated (Schneider et al. 2005). Hence, a male that monopolizes a female above the average body size should gain higher reproductive success than one that fertilizes all eggs of a female at the lower end of the distribution. To evaluate choice based on female mating status and fecundity, we performed a multilevel experiment in which we observed male behaviour (attraction, courtship, copulation) towards females that differed in fecundity-related traits and, in the course of the observation, also in mating status. Experimental females were collected as late penultimates and matured in the laboratory. We then selected pairs of females that differed in body size and weight and presented them simultaneously either to males in the laboratory (inexperienced males) or to roving males in the field. Thus, search and sampling costs were minimized for males. Copulation events that occurred during the observation period allowed us to register changes in female attractiveness that were related to the change in female mating status. We predicted that males would favour the larger female of a pair and prefer virgin over mated females.

METHODS

Collection and Rearing

Males are protandrous and mature before females at a smaller adult size. Subadult males and females of *A. bruennichi* were collected in June 2007 from sites less than 100 km south of Hamburg in northern Germany. In the laboratory, the larger females were initially kept in upturned plastic cups of 400 ml, and the males in smaller ones of 200 ml. All spiders were fed twice a week and watered 5 days a week. Females received two or three *Calliphora* flies and males were fed with *Drosophila* spp. flies ad libitum. All spiders were checked daily for moults so that the exact date of maturation was known. We defined age of a spider as days elapsed from the final moult until the day of the trial. Females were transferred to Perspex frames (30 × 30 cm and 6 cm high) before or immediately after their last moult, while males stayed in plastic cups until the laboratory experiments began. In the frames, females constructed complete orb-webs and mating trials were carried out in these frames. Webs that were present before maturation were destroyed to ensure that females would build a new web after their final moult.

Measurements

After the field and laboratory trials, all males and females were anaesthetized with CO_2, to weigh and/or measure them. To prevent damage to the webs prior to the trials, females were generally weighed and measured after them, while laboratory males were measured afterwards but weighed before trials (measuring is more stressful to the male than weighing). As a measure of body size for both sexes, we used the mean of the left and right tibia–patella length of the first pair of legs, as the legs of spiders are sclerotized body parts that do not change in length after the final moult. The distance was measured in mm with digital callipers (accuracy 0.01 mm). Condition was estimated using the residuals from the regression of weight and size (Schulte-Hostedde et al. 2005). Weight was measured in mg with an electronic scale (Mettler Toledo AB54-S; accuracy ±0.01 mg). Body size was our main target criterion because only size does not change after maturation, while weight and condition increase with age. As size and weight were correlated (Pearson correlation coefficient: $r = 0.75$), we dropped weight as a variable and report results from analyses concerned with body size and condition.