Strategic male mating behaviour in *Argiope lobata*

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In mating systems with strictly limited male mating opportunities, a male's reproductive success depends strongly on the quality of his mate. Female quality is often linked to body size and mass. Hence, males with limited mating opportunities should choose large and heavy females to maximize their reproductive success. However, high-quality females are likely to attract more than one male, which consequently results in male–male competition. This scenario can be found in the spider species *Argiope lobata*. Males can copulate twice at most and eventually die after mating, but can monopolize females through the application of mating plugs. These plugs are costly because males block the female's genital openings with parts of their sperm-transferring organs (pedipalps), rendering them dysfunctional. Plugging moreover increases the risk of sexual cannibalism. We tested whether male *A. lobata* adjust their mating investment to the expected gains, which are a function of female fecundity and the risk of sperm competition. We presented males with virgin females of different fecundity, in either the presence or absence of a rival. Indeed, we found that males were selective and preferred larger females under competitive conditions. When a rival was present and the female was small, males frequently performed ultrashort copulations of less than 3 s without sperm transfer. Ultrashort copulations may imply that males were not willing to invest in paternity under these conditions. In contrast, when two rivals competed for heavy and thus fecund females, males were significantly more likely to monopolize paternity by depositing a plug. In conclusion, our results suggest that males try to adapt their copulatory behaviour to female quality and the degree of sperm competition even in ‘dangerous’ mating systems.

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Sexual selection theory predicts that males should adjust their mating investment to the expected gains, i.e. the expected reproductive success (Bonduriansky, 2001; Parker, 1998; Parker, Ball, Stockley, & Gage, 1996; Wedell, 1991). Expected gains will depend on many factors, such as the degree of competition and a male’s probability of succeeding in competition, as well as the relative quality of the mate and the availability of further mating opportunities (Scharf, Peter, & Martin, 2013). The strength of selection pressures on male behaviour will be influenced by the male mating rate (Barry & Kokko, 2010). Accordingly, strategic male mating investment is particularly expected if males have very limited mating opportunities, so that each decision has a strong impact on fitness (Schneider, 2014). Male mating rates can be limited if the costs of mating are very high, for example through the production of nuptial gifts. Male scorpionflies, *Panorpa vulgaris*, that produce costly salivary donations increase their investment in nuptial gifts with increasing female fecundity (Sauer, Sindern, & Kall, 1997) and here male selectivity is a function of the relative costs (Engqvist & Sauer, 2001). An even more dramatic limitation of male mating rates can be found in monogynous mating systems with sexual cannibalism, for example in spiders (Schneider & Fromhage, 2010). Here, males terminally invest in one or rarely two females before they die. Male mate choice is expected if females vary in quality (Fromhage & Schneider, 2012) and males often compete for access to high-quality females. In contrast to the many studies on species with conventional sex roles, our knowledge about strategic investment of males is still limited in monogynous systems.

In species with multiply mating (= polyandrous) females, males compete not only before but also after copulation by means of sperm competition and cryptic female choice (Eberhard, 1996; Parker, 1970). Many studies have shown that males assess the risk or the intensity of sperm competition and vary their allocation of sperm strategically to maximize reproductive success (Kelly & Jennions, 2011; Wedell, Gage, & Parker, 2002). For example, males of the butterfly *Pieris napi* increase their investment in spermatophore size with increasing sperm competition, but the degree of increase depends on life history trade-offs (Larsdotter-Mellstrom & Wiklund, 2015). Males are also known to plastically

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adapt their efforts to reduce or prevent sperm competition, e.g. through mate guarding. For example, Seychelles warblers, _Acrocephalus sechellenesis_, whiptail lizards, _Aspidoscelis costata_, and wingless ants, _Hypoponera opacior_, increase the intensity or duration of mate guarding under a higher risk of shared paternity (_Ancona, Drummond, & Zaldivar-Rae_, 2010; _Komdeur_, 2001; _Kureck, Neumann_, & _Foitzik_, 2011). However, although mate guarding helps to secure paternity, it can be costly for males as it may result in a higher predation risk (_Hoeksema_, 2008), energy depletion (_Komdeur_, 2001) and missed opportunities to compete for other mates (_Kokko & Jennions_, 2008). A passive form of mate guarding can be achieved via mating plugs, which are effective and economical to avoid sperm competition through hindering or delaying the female’s remating (_Birkhead & Moller_, 1998; _Dunham & Rudolf_, 2009; _Shine, Olsson_, & _Mason_, 2000). This strategy has evolved independently in several taxa, is common in arachnids and even permanent in entelegyne spiders, where insemination openings are independent of oviposition openings (_Uhl, Nessler_, & _Schneider_, 2010). In spiders, the application of high-cost mating plugs is known for several monogamous or bigamous species.

In arachnids, mating plugs are most commonly composed of secretions, but they can also constitute parts of the male genitals. Genital plugs are often accompanied by genital mutilation and this is especially costly because it precludes future mating opportunities (_Uhl et al._, 2010). Male spiders have two secondary mating organs, the pedipalps, and if genitals are damaged during copulation, they can be used only once each, limiting the male to a maximum of two copulations. The existence of such one-shot genitalia is generally associated with a monogamous mating system in which males actively limit their mating effort to a single female (_Schneider & Fromhage_, 2010). Monogamous mating systems in spiders are also associated with sexual cannibalism, which will further limit male mating rates (_Miller_, 2007). Interestingly, plugging may or may not co-occur with sexual cannibalism, which may alter the relative costs of genital plugs (_Boomsma, Baer, & Heinze_, 2005; _Fromhage & Schneider_, 2006; _Hosken & Price_, 2009; _Kuntner, Coddington_, & _Schneider_, 2009; _Miller_, 2007; _Snow, Abdel-Meshil_, & _Andrade_, 2006). Owing to very limited mating opportunities and extreme mating effort, it should be highly advantageous for males to adjust the implementation of their mating strategy precisely to the degree of male–male competition. Most models and studies on strategic male mating investment consider sperm allocation of species with conventional sex roles such as many birds and insects, which differ in many ways from systems with extremely low mating rates (_Scharf et al._, 2013).

The spider species _Argiope lobata_ is an ideal model to study male mating decisions in a mating system with low male mating rates because plugging increases the risk of cannibalism (_Nessler, Uhl_, & _Schneider_, 2009), forcing males to trade off sperm protection against further mating opportunities. The operational sex ratio in _Argiope_ species changes during the mating season, altering the benefits of sperm protection. Thus, plastic mate plugging behaviour seems eminently beneficial (_Foellmer_, 2008; _Welke & Schneider_, 2012; _Welke, Zimmer_, & _Schneider_, 2012; _Zimmer, Welke_, & _Schneider_, 2012). The predictability of this change could enhance the evolution of plastic mating behaviour. If the operational sex ratio becomes male biased, conditions with high risks of sperm competition arise, which may favour the monopolization of females via mating plugs. In contrast, if the operational sex ratio tends to become less male biased towards the end of the season and males may have higher fitness by inseminating more than one female, they should avoid plugging. Since plugging reduces the probability of a male surviving a mating, the balance may tilt towards surviving to mate with other females rather than sperm protection if the risk of sperm competition is low. Note that the conditions of classical sperm competition models (_Parker_, 1970) do not fully apply. Spiders differ from many other taxa including the well-known examples of sperm competition and postcopulatory sexual selection in general because of the paired but independent genital structures and immobile sperm (_Eberhard_, 2004; _Herberstein, Schneider_, _Uhl_, & _Michalk_, 2011).

_Male A. lobata_ use only one pedipalp per copulation event and can break off a part of the pedipalp during mating to form the plug. Thereby, males effectively obstruct the copulatory opening of the female. _Nessler et al._ (2009) detected that about 40% of all _A. lobata_ males damaged their genitals in the act of mating, but only 14% succeeded in lodging a plug. The adaptive value of this strategy for paternity protection is high, as subsequent males that copulate in previously plugged genital openings sire less than 1% of the offspring (_Nessler et al._, 2009). Despite the high efficacy of mating plugs, it is surprising that most males do not seize this opportunity to secure paternity. This may suggest that males possibly use this option according to a cost–benefit ratio, which depends on phenotypic or environmental conditions. Males of the genus _Argiope_ are often monogamous, even though they have the possibility to mate with a second female (_Herberstein, Wignall, Nessler, Harmer_, & _Schneider_, 2012; _Welke & Schneider_, 2009). In _A. lobata_, a male’s chancier bigamy can be diminished by plugging, as it often co-occurs with sexual cannibalism (_Nessler et al._, 2009).

In this study, we focused on male plugging to explore the plasticity of the reproductive behaviour of _A. lobata_. We simulated a condition with an increased sperm competition risk by exposing a virgin female to two competing males simultaneously. One of the males was an unmated intact male, while the competitor was an experimental eunuch. Eunuchs were made impotent by inducing autotomy of the pedipalps and remained motivated to mate. As documented in other studies (_Nessler, Uhl_, & _Schneider_, 2007; _Rovner_, 1967; _Schneider & Lesmono_, 2009; _Welke & Schneider_, 2009), eunuchs in this study behaved like a true rival and initiated competitive interactions and even fights. This set-up made sure that the mating male was predetermined and achieved the copulation independent of his competitive abilities. By comparing mating efforts of males in the two treatments, we tested the hypothesis that males adjust their mating behaviour strategically to an increased risk of sperm competition.

Yet, as mentioned above, the contributions of each sex towards aspects of mating remain unclear. If mating is under male control, we expected males to skip courtship under competitive conditions as they do in the congner _Argiope bruennichi_ (_Schneider & Lesmono_, 2009). Alternatively, males may prolong courtship if mate acceptance by the female directly depends on courtship effort (_Stoltz, Elias, & Andrade_, 2008). Moreover, in trials with competitors we predicted males would respond with higher plugging rates and prolonged copulations, to increase investment in paternity (_Kelly & Jennions_, 2011). In this context, we used female quality as a covariate that might change the cost–benefit ratio of plugging. As generally true for arthropods, female fecundity is indicated through size and weight, which are proposed to be important cues for shifts in mating behaviour (_Ancona et al._, 2010; _Reinhold, Kurtz_, & _Engovost_, 2002; _Zimmer et al._, 2012). Especially for monogamous males, fecundity of the female is of particularly high relevance for fitness. Accordingly, we predicted that male decisions over investment in plugging would be affected by female size.

**METHODS**

**Study Animals**

Eight eggsacs and six adult mated females of _A. lobata_ were collected in September 2009 in the Nitzanim dunes between

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