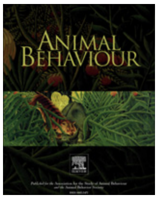
Animal Behaviour 82 (2011) 1201–1206

Contents lists available at SciVerse ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Perceived risk of sperm competition affects juvenile development and ejaculate expenditure in male praying mantids

Louise E. Allen[a], Katherine L. Barry[a,*], Gregory I. Holwell[b,1], Marie E. Herberstein[a]

[a] *Department of Biological Sciences, Macquarie University*
[b] *School of Biological Sciences, Auckland University*

A R T I C L E I N F O

Article history:
Received 6 July 2011
Initial acceptance 3 August 2011
Final acceptance 31 August 2011
Available online 28 September 201128
September 2011
MS. number: 11-00534

Keywords:
developmental plasticity
ejaculate expenditure
praying mantid
Pseudomantis albofimbriata
sex ratio
sperm competition
sperm transfer

Sperm competition occurs when a female mates with more than one male, and the sperm of those males compete directly over fertilizing her eggs. In polyandrous animals, males can respond to the perceived risk of sperm competition by flexibly adjusting aspects of their development and reproductive investment. In high-risk scenarios we might expect males to accelerate development so as to mature quickly and locate receptive females first and/or transfer more sperm so as to outcompete rival sperm. We examined these predictions using the false garden mantid, *Pseudomantis albofimbriata*, a medium-sized praying mantid found on the east coast of Australia. Males are less than half the mass of females. Sexual cannibalism occurs in up to 40% of interactions, highlighting the importance of investing optimally in reproductive opportunities for males. We housed juvenile males in two operational sex ratio treatments: three males, one female (high risk of sperm competition) and one male, three females (low risk). We found no evidence of accelerated development in the high-risk group; instead, high-risk males took longer to mature. Possibly, males exposed to a higher risk of sperm competition delay maturity in order to invest in testes development and sperm production. We also found that males reared in the high-risk treatment transferred significantly more sperm than males reared in the low-risk treatment, providing evidence of strategic ejaculation in male *P. albofimbriata*. This is the first study demonstrating a male response to the perceived risk of sperm competition via delayed development and increased ejaculate investment in praying mantids.

Females of many species are polyandrous and may as such gain direct benefits including nutrients transferred in the ejaculate, access to resources such as oviposition sites, and replenished sperm reserves (Parker 1982; Simmons 2001), along with indirect genetic benefits (reviewed in Jennions & Petrie 2000). It is therefore not surprising to find numerous and diverse adaptations in males either to avoid sperm competition entirely (defensive strategies) or to outcompete competitors once engaged in sperm competition (offensive strategies; Simmons 2001). These adaptations are often observed in insects because females have a tendency to mate multiple times and store sperm in specialized organs (Simmons 2001). As a result, male insects frequently experience elevated levels of sperm competition compared to other taxa (Simmons & Siva-Jothy 1998).

Defensive strategies are those used to avoid sperm competition with other males completely (Simmons 2001), most commonly: pre- and postcopulatory mate guarding, mating plugs and strategies that facilitate the rapid location of virgin females (Arnqvist 1988; Simmons 2001). It is common for males to use a combination of these, and so multiple strategies often occur within a single mating system (Watson et al. 1998; Simmons 2001). Male water striders, *Gerris lateralis*, guard females after copulation by 'riding' on the female's back (Arnqvist 1988). This behaviour seems to have arisen as a response to females storing sperm for long periods without any decrease in viability, for over 30 days in *G. lateralis* (Arnqvist 1988, 1989; Rubenstein 1989; Watson et al. 1998). The sperm received from one mating is in fact enough to fertilize all eggs without a second mating during the mating period (Arnqvist 1989, 1998; Rubenstein 1989). Female sperm storage and the high levels of male competition seem sufficient to promote the expenditure of lengthy mate guarding as an effective way to avoid sperm competition in these water striders (Arnqvist 1988, 1989;

---

* Correspondence: K. L. Barry, Department of Biological Sciences, Macquarie University, North Ryde, Sydney, NSW 2109, Australia.

E-mail address: kate.barry@mq.edu.au (K. L. Barry).

[1] G. I. Holwell is at the School of Biological Sciences, Auckland University, Auckland 1142, New Zealand.

0003-3472/$38.00
doi:10.1016/j.anbehav.2011.09.009

Rubenstein 1989; Watson et al. 1998). Male redback spiders, *Latrodectus hasselti*, use mating plugs as a defensive strategy to reduce the threat of sperm competition. Female redback spiders mate multiply and have two copulatory openings (Andrade 2003; Snow & Andrade 2004; Snow et al. 2006), and male redbacks use their sperm transfer organs, the pedipalps, as mating plugs (Snow et al. 2006). The male endures the risky mating with his sexually cannibalistic partner only to cease copulation and leave his pedipalp blocking the female's genital tract. If the male is able to survive the first copulation he will attempt another, into the second female copulatory opening. Consequently, if a male can block both female openings he has a higher probability of completely impeding rival sperm (Andrade 2003; Snow & Andrade 2004; Snow et al. 2006).

Offensive strategies are used in the presence of rival sperm (Simmons & Siva-Jothy 1998; Simmons 2001). In most cases males outcompete other males by displacing rival sperm (Snook & Hosken 2004), transferring secretions that either promote sperm usage or influence cryptic female choice (Boer et al. 2008, 2010), or by transferring substances that destroy rival sperm (Simmons & Siva-Jothy 1998; Simmons 2001). As with defensive strategies, it is common to use a combination of offensive strategies within a single mating system (Simmons & Siva-Jothy 1998; Simmons 2001). One of the most common offensive strategies used by males to ensure successful paternity is simply to transfer more sperm. This strategy allows for sperm defects, displaces rival sperm or fills sperm storage organs, increasing the chance of successful fertilization in the presence of sperm competition (Parker 1982; Simmons & Siva-Jothy 1998). For example, male bush crickets, *Requena verticalis*, that mate with older females transfer 50% more sperm than with younger females (Simmons et al. 1993). This strategy has arisen as older females are more likely to have already mated and thus males are responding to the perceived higher level of sperm competition (Simmons et al. 1993).

Adult males regularly use combinations of defensive and offensive strategies such as those mentioned so far, but it is interesting also to consider whether juveniles can respond to the threat of sperm competition. This requires juveniles to detect population density and sex ratio and have the ability to alter their development and adult size by speeding up or slowing down their growth rate (Kasumovic & Andrade 2006). As a result of juvenile experience, males may 'race' to females, referred to commonly as scramble competition. Winning the race to a female can be achieved in two ways. First, males may speed up development and/or mature as smaller individuals, as small males may be more agile than large males (Dunn et al. 1999; Vencl 2004; Kasumovic & Andrade 2009; Moya-Larano et al. 2009) and maturing early may provide a window of opportunity to obtain matings while other males are still developing (reviewed in Andersson 1994; Kasumovic & Andrade 2006). Second, delaying development and maturing as a larger male might provide the ability to race to females faster or overpower other males in physical contests (Carroll & Salamon 1995; Hanks et al. 1996). Male redback spiders show a condition-dependent shift between these developmental strategies (Kasumovic & Andrade 2006). When females are absent, males trade off rapid development for increased body size/condition, as larger males in better condition are more likely to survive mate searching and direct physical competition. In contrast, males trade off size and body condition for rapid development when females are present, which is likely to improve their chances of maturing and reaching virgin females first (Kasumovic & Andrade 2006).

Praying mantids are an ideal group in which to investigate the response to sperm competition because females are capable of multiple copulations (Barry et al. 2011; Watanabe et al. 2011) and store sperm in a sac-shaped spermatheca (Winnick et al. 2009; K. L. Barry, unpublished data); numerous males are often simultaneously attracted to the pheromones emitted by a single female (Lelito & Brown 2008; Barry 2010; Maxwell et al. 2010a,b). Fluctuations in development time, predation rates and the frequency of sexual cannibalism can have a significant effect on the population sex ratio (Hurd et al. 1994), with late-maturing males having fewer females to choose from but also fewer competitors for those females. There is also evidence that female mantids become chemically unattractive (or at least less attractive than virgins) in many species (Robinson & Robinson 1979; Gemeno et al. 2005; Perez 2005; Lelito & Brown 2008; Barry et al. 2011), which may mean that the ability to respond to varying levels of sperm competition is not quite as important for male mantids as first thought.

In the current study, we used the sexually cannibalistic false garden mantid, *Pseudomantis albofimbriata*, to investigate whether males are able to detect the risk of sperm competition as juveniles and respond accordingly. A previous study showed that the intense scrambling behaviour exhibited by males in this species is probably due to the complete cessation of female pheromone production once mated (Barry et al. 2011). We therefore might expect males to respond to the increased risk of scramble competition by maturing early so as to arrive at females sooner. However, as in many insects with sac-shaped spermathecae (Simmons 2001), last-male sperm precedence occurs in *P. albofimbriata*, with the second male to mate fertilizing twice as many eggs as the first male to mate with a female (Barry et al. 2011). This may mean that males maturing and arriving at females later will still have the advantage in sperm competition. Our first aim in this study was therefore to determine whether males are able to adjust particular aspects of their juvenile development (i.e. rate of development and size at maturity) in response to the perceived risk of sperm competition. Second, we aimed to determine whether males respond to the risk of sperm competition by adjusting their ejaculate expenditure during copulation.

METHODS

Collection, Housing and Rearing

Mantid nymphs were collected from December 2009 to February 2010. Collection sites were located in Sydney, Australia and included Bicentennial Park at West Pymble, Turramurra and North Ryde. Individuals were of various ages at the time of collection and ranged from first instars to antepenultimate subadults. Each mantid was housed individually in an inverted plastic cup (425 ml) with the base removed and replaced with mesh to allow airflow. Juveniles were fed 10–20 *Drosophila melanogaster* three times a week. Larger juveniles were fed a combination of *D. melanogaster* (ca. 5–10) and small crickets, *Acheta domestica* (ca. 1) per week. Subadult and adults were fed two to three small *A. domestica* three times a week. Laboratory conditions were kept at a constant temperature of 25 °C with a 12:12 h day:night cycle.

Treatment Allocation

Individuals were assigned to male-biased (i.e. high risk of sperm competition) or female-biased (i.e. low risk of sperm competition) treatments as soon as they could be sexed (last two instars). These treatments were established by creating groups of four cups each with a resident mantid. Each group contained four individuals that were visible to each other but visually obscured from other groups. The set-up also allowed transfer of any chemical cues between groups so that males were able to receive male and female cues visually and chemically. Treatments were placed in separate rooms