Ejaculate expenditure by male bushcrickets decreases with sperm competition intensity

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SUMMARY

Male bushcrickets transfer a spermatophore at mating that consists of a sperm-containing ampulla and a sperm-free mass, the spermatophylax, that is consumed by the female during insemination. The costs of spermatophore production for males and benefits of consumption for females result in reversals in courtship roles in nutrient-limited populations that increase both the risk and intensity of sperm competition. Here we show that under conditions characteristic of courtship role reversal, male expenditure on the spermatophore is dependent on female size. When mating with small females, males increase the amount of spermatophylax material and sperm, as expected from the increased sperm competition risk associated with courtship role reversal. However, males reduce the amount of spermatophylax material and sperm transferred to larger females. Since larger females have a higher mating success when competing for nurturant males, the intensity of sperm competition covaries with female size. Reduced ejaculate expenditure under increased sperm competition intensity is in accord with theoretical expectation.

1. INTRODUCTION

Courtship feeding, the donation of a food gift by males to females during copulation, is widespread in insect taxa (Thornhill & Alcock 1983). Food gifts can include prey items (Thornhill 1976), the products of male metabolism (Gwynne 1984; Mullins *et al.* 1992), specially adapted male body parts (Sakaluk & Snedden 1990), and, in sexually cannibalistic species, the male himself (Andrade 1996). The evolution of courtship feeding has been extensively studied and the evidence supports both a role of sexual selection for increased male fertilization success and natural selection for increased male parental investment (Simmons & Parker 1989).

One common factor in these arguments is the role of sperm competition. When females mate multiply, the sperm from two or more males will compete for available ova (Parker 1970). Thus courtship feeding can evolve through sexual selection if it facilitates the transfer of greater numbers of sperm that increase a male's paternity expectation (Sakaluk 1986; Wedell 1991; Andrade 1996). Natural selection is only expected to favour the evolution of male parental investment where there is a high confidence of paternity (Westneat & Sherman 1993). Thus, increased male parental investment should be associated with mechanisms that enhance the investing male's paternity. In paternally investing water bugs and burying beetles, paternity assurance mechanisms involve the transfer of large numbers of sperm through repeated copulations that enhance success in sperm competition (Smith 1979; Muller & Eggert 1989).

Male bushcrickets feed their mates with a product of the accessory gland, the spermatophylax, that is attached to the sperm-containing ampulla of the spermatophore, that is transferred to the female at copulation (Boldyrev 1915). The ejaculate of bushcrickets thus comprises sperm and seminal fluid, as well as accessory secretions associated with the spermatophore complex. Recent studies have shown that the spermatophylax functions both in ensuring sperm transfer and fertilization success, and in providing the female with nutrients that increase the number and fitness of offspring produced (Gwynne 1984; Simmons 1990, 1995a; Simmons & Gwynne 1991; Wedell 1991, 1994a). Production of the spermatophore can represent a significant cost of reproduction in terms of the time required to recover from a given reproductive event (Simmons 1995c). For at least three species, spermatophore production costs have been shown to result in a reversal in courtship roles (Gwynne 1981, 1985, 1993; Gwynne & Simmons 1990).

For *Kawanaphila nartee*, courtship roles depend on the availability of resources in the environment (Gwynne & Simmons 1990; Simmons & Bailey 1990; Simmons 1995c). When resource availability is high, male remating rate is high while females rarely mate more than once. Thus the operational sex ratio (OSR *sensu* Emlen & Oring 1977) is biased toward an excess of males that compete for access to females. In contrast, as resources become limited, female remating rate increases as they forage for matings and the resources that males offer (Simmons & Gwynne 1991). Males, however, have a greatly reduced remating rate so that the OSR becomes biased toward

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an excess of receptive females. Mating competition among females for multiple mating partners is intense. Sperm from successive matings are stored by the female and compete numerically for fertilizations (Simmons 1995c). Thus, despite the female-biased OSR, the inevitable consequence of courtship role reversal for males is that both the risk of sperm competition (probability that a male will be in direct competition for fertilizations) and the intensity of sperm competition (number of males with which an individual must compete for fertilizations) are increased.

Theoretical investigations have shown that selection should favour adaptive responses in ejaculation strategies as the risk of sperm competition increases (Parker 1990a,b). Across species, increased risk of sperm competition is predicted to favour increased investment in gametogenesis. Thus, species which have high risks of sperm competition have relatively larger testes (Harcourt *et al.* 1981; Ginsberg & Rubenstein 1990; Møller 1991; Gage 1994; Stockley *et al.* 1997). Within species, males have been shown to increase the numbers of sperm in relation to their perceived risk of sperm competition (Gage 1991; Gage & Baker 1991; Simmons *et al.* 1993; Cook & Gage 1995; Gage & Barnard 1996). However, more recent models predict that increased intensity of sperm competition within species should result in decreased sperm numbers (Parker *et al.* 1996). No empirical data are yet available to test this prediction. Here we examine the ejaculation strategies of *K. nartee* while experimentally manipulating the conditions characteristic of conventional and courtship role-reversed populations. We interpret our findings in the light of the recent predictions of Parker *et al.* (1996) for increased risk and intensity of sperm competition.

2. METHODS

Animals to be used in experiments were collected from Kings Park, an area of native bushland in the centre of metropolitan Perth. Females were collected as penultimate instar nymphs and reared to adulthood in stock cages containing freshly cut spring flowers as a food source. Cages were misted with water daily and adult females removed and housed individually in 250 ml jars. Females were not used in mating trials until they were three weeks of age. Experimental males were collected as sexually active adults, determined by the fact that they were calling to attract females on the night of capture. Males were collected five days before experiments and housed individually. All animals were housed on a 12 h (19 °C) light:12 h (10 °C) dark cycle. We performed two separate experiments in which we simulated the conditions that would be experienced by males in conventional and courtship role-reversed populations.

(a) *Female encounters*

Reversal in courtship roles is characterized by an increase in male choosiness. Shelly & Bailey (1992) have shown that *K. nartee* switch to exercising mate choice when their encounter rate with potential mating partners is high. We thus adopted the method of Shelly & Bailey

(1992) to manipulate male courtship roles. Males were allocated at random to one of two treatment groups. In the first, males were allowed to encounter non-experimental females for a period of 3 h on each of four successive nights. Thirty minutes prior to the dark cycle, three adult females were placed into each male's jar. Animals were checked regularly. Pairs found in precopula were gently separated by pulling the female from the males back. This procedure simulated female take-overs that occur naturally in courtship role reversed populations (Simmons & Bailey 1990; Gwynne & Simmons 1990). Thus, the males in this group had multiple encounters with sexually active females prior to experimental pairing. The remaining males were kept isolated from females on the four nights prior to experiments. All males were housed in glass jars with sealed lids, so preventing acoustic interactions between neighbours. Since males were allowed to interact with females only, the perceived OSR during this experiment was female biased in all treatments.

On the fifth night, 30 min before the dark cycle, a single female was placed into each male's jar and the pair observed for a period of 4 h or until spermatophore transfer. Male and female body sizes were measured as the length of the pronotum, and body weights were determined to an accuracy of 0.1 mg.

(b) *OSR and variance in mate quality*

The ultimate factor controlling the operation of sexual selection via mating competition is the OSR (Kvarnemo & Ahnesjö 1996; Parker & Simmons 1996). In contrast, sexual selection via mate choice is thought to be controlled also by variance in mate quality (Owens & Thompson 1994; Johnstone *et al.* 1996). In our second experimental manipulation, we examined the influence of OSR and mate quality on ejaculate expenditure. In this experiment we randomly allocated males to a pre-treatment consisting of either a male-biased or a female-biased OSR. For the male-biased OSR we housed experimental males in groups of three. Males were housed in plastic vials with fly screen windows and lids that allowed transmission of acoustic signals. For the first 3 h of the dark cycle, their vials were interspersed with vials containing five sexually signalling non-experimental males. Calling activity was checked every 30 min using a QMC bat detector (songs have a peak carrier frequency of 50 kHz). The males sang continuously with a high pulse repetition rate indicating that they were interacting acoustically with each other (Simmons & Bailey 1993). For the female-biased OSR, males were housed individually and their vials separated by sound absorbing barriers (6 cm thick blocks of compressed paper). The males in this treatment sang sporadically and with a slow pulse repetition, indicating that they were not interacting (Simmons & Bailey 1993). For the first 3 h of the dark cycle, males in the female bias treatment were exposed to three sexually active non-experimental females as described above. The pre-treatment period for this experiment lasted for three nights.

On the fourth night, all males were housed individually and randomly assigned a sexually receptive female derived from one of two treatment groups; females were either of high or low variance in quality. We manipulated variance in female quality by manipulation of female diet, and thus fecundity. From the day of adult eclosion, females were provided with pollen, either *ad libitum*, on every second day, or on every third day. Females for the low variance treatment were all taken from those fed on every second day. Females for the high variance treat-

ment were taken in equal numbers from each of the diets. Our manipulations influenced fecundity; the variance in fecundity differed between treatments ($F_{(21,27)} = 2.48$, $P = 0.01$) but the mean fecundity did not ($t = 0.863$, d.f. = 33.8, $P = 0.39$; mean $\pm$ s.d. number of eggs in ovaries for high variance, 16.4 ± 8.3 , and low variance, 14.6 ± 5.3). Pairs were observed for 4 h or until spermatophore transfer. Male and female body sizes were measured as the length of the pronotum and body weights determined to an accuracy of 0.1 mg.

(c) Ejaculate characteristics

Spermatophores were removed from the female immediately following copulation. The spermatophylax was dissected from the ampulla and the mass of each component determined. Variation in sperm number was estimated using spermatophores obtained from the first experiment only. The ampulla was placed into 20 ml of particle-free water and ruptured. An homogenous mix was made by constant mixing. We withdrew two 20 μ l samples and placed them onto a clean, dry microscope slide. Three slides were made per ampulla, providing six sperm counts. Once dry, sperm counts were made under dark field phase contrast.

3. RESULTS

(a) Ejaculate characteristics

There was a positive relation between the weight of the ampulla and the weight of spermatophylax material transferred ($F_{(1,89)} = 87.89$, $P < 0.001$; figure 1). The spermatophylax represents on average $47.1 \pm 0.01\%$ ($n = 91$) of the spermatophore. Spermatophores contained an average of 3.73 ± 0.44 million sperm and heavier ampullae contained more sperm ($F_{(1,38)} = 7.411$, $P = 0.009$). Ejaculate characteristics were dependent on male body weight, so we calculated residuals from regressions of ampulla and spermatophylax weights on male body weight for analyses of male ejaculate expenditure in relation to our experimental manipulations (regression statistics for data combined across experiments, ampulla weight $F_{(1,89)} = 44.44$, $P < 0.001$; spermatophylax weight $F_{(1,89)} = 76.12$, $P < 0.001$).

(b) Female encounters

We used a one-factor analysis of covariance to examine the influence of prior encounters with females and female body size on ejaculate characteristics, following the procedure of Hendrix *et al.* (1982), with an $\alpha \leq 0.1$ to avoid type II errors in the detection of interactions. For residual spermatophylax weight, there was no significant interaction between treatment and female body size so that the interaction term was removed from the model. Previous encounters with females had no influence on the weight of spermatophylax material transferred by the male, although males transferred smaller spermatophylaxes to larger females (prior encounters, $F_{(1,35)} = 0.07$, $P = 0.79$; female pronotum length, $F_{(1,35)} = 4.21$, $P = 0.048$; figure 2). Neither prior encounters with females or female size influenced residual ampulla

Figure 1. The relation between the weight of spermatophylax material and the weight of the sperm-containing ampulla of the spermatophore of *Kawanaphila nartee*. Larger symbols represent multiple data.

Figure 2. Weight of spermatophylax material transferred to females of increasing body size, after controlling for variation in male body weight (data pooled across female encounter treatments).

weight (prior encounters, $F_{(1,35)} = 0.34$, $P = 0.57$; female pronotum length, $F_{(1,35)} = 0.12$, $P = 0.74$). The interaction term was not significant and was removed from the model.

(c) OSR and variance in mate quality

We used a two-factor analysis of covariance to examine the influence of OSR, variance in mate quality, and female size on ejaculate characteristics. For residual spermatophylax weight, there was a significant interaction between OSR and female size ($F_{(1,43)} = 4.99$, $P = 0.03$) and between variance in female quality and female size ($F_{(1,43)} = 4.68$, $P = 0.03$). All other interaction terms were non-significant and removed from the model. Under a female-biased OSR and when variance in female quality was high, males reduced spermatophylax weight with increasing female size (figure 3). Spermatophylax weight was unaffected by female size under a male-biased OSR and with low variance in female quality. For residual ampulla weight, there was a significant interaction between OSR and female size ($F_{(1,44)} = 5.07$, $P = 0.03$). All other interactions were non-significant and removed from the

Figure 3. Weight of spermatophylax material transferred to females of increasing body size, controlling for variation in male body weight: (a) under conditions of a female-biased OSR; (b) when variance in female quality was high.

Figure 4. Weight of ampullae transferred to females of increasing size, controlling for variation in male body weight, under conditions of a female-biased OSR.

model. Under a female-biased OSR, males reduced the weight of the ampulla with increasing female size (figure 4).

Because of the significant interactions between treatment effects and the covariate, interpretation of main effects cannot be restricted to the mean value for the covariate. We thus examined treatment effects at the mean and at ± 1 s.d. from the mean value for the covariate (see Hendrix *et al.* 1982). When mating with small females, males increased spermatophylax weight under a female-biased OSR; the adjusted mean residual spermatophylax weight 1 s.d. below the mean was -2.678 under a male-biased OSR,

compared with 8.081 under a female-biased OSR ($F_{(1,43)} = 5.49$, $P = 0.024$). Because spermatophylax weight decreased with female size, the effect of OSR was no longer significant at the mean ($F_{(1,43)} = 1.38$, $P = 0.245$) or 1 s.d. above the mean ($F_{(1,43)} = 0.67$, $P = 0.416$). The same was true for ampulla weight; the adjusted mean residual ampulla weight 1 s.d. below the mean was -3.916 in the male-biased OSR, and 4.826 in the female-biased OSR ($F_{(1,44)} = 3.24$, $P = 0.07$), but did not differ significantly at the mean ($F_{(1,44)} = 0.10$, $P = 0.748$) or 1 s.d. above the mean ($F_{(1,44)} = 2.07$, $P = 0.157$). For variance in female quality, residual spermatophylax size did not differ between high and low variance treatments 1 s.d. below the mean ($F_{(1,43)} = 0.83$, $P = 0.826$), but became increasingly smaller in the low variance treatment, at the mean (-1.931 vs 2.197 , $F_{(1,43)} = 3.42$, $P = 0.07$) and 1 s.d. above the mean (-9.807 vs 2.436 , $F_{(1,43)} = 8.79$, $P = 0.005$).

4. DISCUSSION

We found that when experiencing a female-biased OSR and high variance in mate quality, conditions that are characteristic of courtship role reversal, male *K. nartee* reduced their ejaculate expenditure when copulating with large females. Reduced expenditure was manifest predominantly as a reduction in the weight of spermatophylax material attached to the ampulla of the spermatophore, and, to a lesser extent by a reduction in the weight of the ampulla, and thus sperm number.

In our first experiment we found that encounters with females *per se* had no influence on ejaculate expenditure. This result is consistent with previous findings in another species of bushcricket, *Requena verticalis* (Simmons 1995b). In our first experiment, males were not allowed to interact with each other so that the perceived OSR was female biased. In our second experiment, males experiencing the female-biased OSR were similarly prevented from interacting with other males and we were able to replicate the result that males reduced spermatophylax weight when mating with larger females. However, when males were allowed to interact physically and acoustically, so that the perceived OSR was male biased, they did not reduce spermatophylax weight when mating with larger females. These results suggest that it is the interaction with other males that is important in influencing ejaculate expenditure, rather than an assessment of the availability of females. Recent work with walnut flies, *Rhagoletis juglandis*, similarly demonstrated that male density had the greater influence on copulation duration than did female density (Alonso-Pimentel & Papaj 1996).

Available evidence suggests that the bushcricket spermatophore has evolved under sexual selection generated via sperm competition. Following spermatophylax consumption the female removes and consumes the ampulla of the spermatophore. Consumption of the spermatophylax thus delays the female from removing the ampulla before sperm have

been transferred to the spermatheca (Wedell & Arak 1989; Reinhold & Heller 1993; Wedell 1993; Heller & Reinhold 1994; Simmons 1995a). Larger spermatophylaxes take longer to consume (Simmons 1995a). Thus, the amount of spermatophylax material provided covaries with ejaculate size, both across species (Wedell 1993; Vahed & Gilbert 1996) and within species (Wedell & Arak 1989; Wedell 1994b). Spermatophylax weight and ampulla weight were found to covary in this study of *K. nartee*, and previous work has shown that the duration of ampulla attachment is directly proportional to the number of sperm transferred (Simmons & Gwynne 1991). Thus, when males reduce their ejaculate expenditure they will effectively reduce the numbers of sperm inseminated because of reductions in the time available for the transfer of sperm from the ampulla and because of reductions in the numbers of sperm contained within smaller ampullae.

Our results may at first appear counterintuitive. Sperm competition should be more important under courtship role reversal because of increased female remating. Yet males respond by reducing ejaculate expenditure. However, the recent theoretical analyses of Parker *et al.* (1996) make a distinction between sperm competition risk and intensity. They show that both within and across species, ejaculate expenditure should increase with sperm competition risk, a prediction that has much empirical support (Harcourt *et al.* 1981; Ginsberg & Rubenstein 1990; Møller 1991; Gage 1991, 1994; Cook & Gage 1995; Stockley *et al.* 1997). Increases in sperm competition intensity similarly predict increases in ejaculate expenditure across species, although within species predictions differ. As the number of males in competition for a given batch of eggs increases beyond two, each male should invest less in its ejaculate because the benefits arising from a given unit of expenditure will decrease (Parker *et al.* 1996). When *K. nartee* are courtship role reversed, females compete for multiple matings and there is a positive relation between female size and mating success (Gwynne & Simmons 1990; Simmons, unpublished data). Thus, sperm competition intensity covaries with female size so that males should expend less on their ejaculates when copulating with large females. Wedell (1992) has also found that males of the bushcricket, *Decticus verrucivorus*, transfer smaller spermatophores to previously mated females. The models of Parker *et al.* (1996) were originally derived for external spawners in which sperm competition conforms to a simple raffle. Although fertilization is internal, sperm competition in *K. nartee* similarly conforms to a raffle in which each male gains an equal proportion of fertilizations (Simmons 1995c). The same is true for *D. verrucivorus* (Wedell 1991). Under these conditions, the models of Parker *et al.* (1996) will also apply to internal fertilizers (G. A. Parker, personal communication).

Our data also support the prediction that within species, males should increase ejaculate expenditure with increased risk of sperm competition. Female-biased OSR's arise because of female remating, and

are thus associated with an increased risk of sperm competition (Gwynne & Simmons 1990). We found that for small females, males did transfer a larger spermatophylax and ampulla in the female-biased OSR compared with the male-biased OSR. However, the decline in ejaculate expenditure with increased intensity of sperm competition expected with larger females, was sufficient to counter the increased expenditure due to greater sperm competition risk. Our data thus provide empirical support for the within-species prediction that, while increased sperm competition risk should favour increased ejaculate expenditure, increased sperm competition intensity should favour decreased ejaculate expenditure.

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