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Strategic male mating effort and cryptic male choice in a scorpionfly

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In animal species with high male mating effort, males often find themselves in a dilemma: by increasing their mating effort, the gain from each copulation increases but simultaneously reduces available resources and, thus, the opportunity for future copulations. Therefore, we expect males to spend less reproductive resources on matings that provide low reproductive potential, thereby saving resources for future copulations, possibly with high-quality females, a sort of cryptic male choice. However, the strength of the trade-off between investment in a current mating and resources available for future matings must not be the same for all males. Males with relatively high mating costs should allocate their limited resources more cautiously than males with more plentiful resources. Here, we examine this prediction in the scorpionfly *Panorpa cognata*. Prior to copulation, males produce a large salivary mass on which females feed during copulation. We show that the production of larger salivary masses leads to longer copulations. Moreover, the size of the salivary gland and salivary mass increases with increasing male condition. However, males in poor condition make a relatively higher mating investment than males in good condition. We therefore expect male condition to influence cryptic male choice. In accordance with our hypothesis, only males in poor condition choose cryptically, producing larger salivary masses in copulations with females of high fecundity.

Keywords: copulation duration; nuptial gift; *Panorpa*; sexual selection; sperm competition

1. INTRODUCTION

In most animal species males compete for access to reproductive females, whereas females often choose among competing males (Trivers 1972). This difference between the sexes is probably due to the fact that females benefit less from multiple matings than males (Bateman 1948). However, in some species where males provide nuptial food gifts (Vahed 1998) male-donated nutrients contribute substantially to female reproductive success (e.g. Gwynne 1984; Simmons 1988; Wiklund *et al*. 1993; Reinhold 1999). Occasionally, this results in a reversal of sex roles with females competing for nutrient-donating, choosy males (e.g. Gwynne 1981; Simmons & Bailey 1990; Gwynne & Bailey 1999). Another situation where we may expect males to discriminate, though without females being competitive, is when male mating effort (*sensu* Low 1978) is high (Dewsbury 1982; Forsberg 1987). If resources for mating are limited, males should allocate these resources prudently across successive matings in order to maximize the number of offspring.

A crucial prerequisite for the assumption of strategic allocation of mating resources is that mating effort is considerable and, hence, has a strong influence on potential mating effort in future matings. If relative mating effort (i.e. actual mating effort in relation to the energy resources available for matings) is low, there will be no or only a weak trade-off between mating effort in the current mating and future matings. Consequently, males will not benefit from regulating their mating effort in relation to the quality of the female mating partner (cf. Parker 1998). Therefore, we only expect strategic allocation of mating resources in species where the relative mating effort is high. However, not all males within a species have the same amounts of resources so the opportunity for future matings will be different. Consequently, the importance of every single mating differs between males. We therefore expect male choosiness to increase with relative mating effort. Males whose relative mating effort is high should invest more mating resources in copulations with high-quality females. Males with low mating costs should be relatively indiscriminate concerning the quality of females. In order to test these predictions we analysed male mating effort in relation to female condition in the scorpionfly *Panorpa cognata* Rambur (Insecta: Mecoptera).

Like other scorpionflies, males of *P. cognata* initiate copulations by offering females a nuptial food gift on which females feed during copulation. In many insect species, nuptial food gifts function as mating effort. The provision of larger nuptial gifts results in copulations of longer duration enabling the transfer of more sperm (for a review, see Vahed 1998). Apart from the salivary masses of scorpionflies (Thornhill 1979; Thornhill & Sauer 1991; Sauer *et al*. 1997, 1998), this function of nuptial food gifts is known for nuptial prey in hangingflies (Thornhill 1979, 1983) and dance flies (Svensson *et al*. 1990), external glandular secretions in a ground cricket (Bidochka & Snedden 1985), and the spermatophylax of several bush-crickets (Gwynne *et al*. 1984; Wedell & Arak 1989; Simmons & Gwynne 1991; Reinhold & Heller 1993; Simmons 1995) and crickets (Sakaluk 1984, 1985). If the function of the nuptial gift is to maximize sperm transfer, the optimal allocation of resources should follow predictions from sperm competition theory (for a review, see Parker 1998). If females differ in fecundity, the intensity of sperm competition (cf. Parker *et al*. 1996) per egg will of course decrease with increasing number of eggs. Thus,

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the expected gain of an increase in mating expenditure will be higher in copulations with fecund females than in copulations with females that only have few eggs to fertilize. In other words, the probability that an increase in male mating effort results in more sired offspring will increase with increasing female fecundity. Consequently, if male mating resources are limited, it will always pay males to invest more in matings with females of high fecundity than in copulations with low-quality females.

The importance of female fecundity on male mating effort has been emphasized by recent research (Gage & Barnard 1996; Sauer 1996; Sauer *et al*. 1997, 1998; Gage 1998; Galvani & Johnstone 1998; Parker *et al*. 1999; Wedell & Cook 1999). For instance, males of the dung fly *Scatophaga stercoraria* copulate longer and, hence, displace more rival sperm in copulations with females containing more eggs (Parker *et al*. 1999) and males of the scorpionfly *Panorpa vulgaris* are more likely to offer costly nuptial gifts and, consequently, increase copulation duration and sperm transfer in copulations with high-quality females (Sauer 1996; Sauer *et al*. 1997). Similarly, males increase mating effort, measured as sperm number, in copulations with more fecund females in the Indian meal moth *Plodia interpunctella* (Gage 1998), the cricket *Gryllodes supplicans* (Gage & Barnard 1996) and the small white butterfly *Pieris rapae* (Wedell & Cook 1999).

The scorpionfly *P. cognata* offers excellent opportunities for testing hypotheses concerning optimal male mating effort. Male mating investment is high. Simultaneously, females are polyandrous, thereby creating intense sperm competition. After the attraction of a female, males court females for an extensive period of time before they initiate copulation by producing a salivary mass. In some cases, premating periods of 7 h have been recorded. This nuptial gift, which is secreted from the salivary gland, is consumed by females during copulation. Alternatively, in some cases a dead arthropod is provided as a nuptial gift. In contrast to related species that continue to produce salivary masses throughout copulation (cf. Sauer *et al*. 1998), as a rule, males of *P. cognata* secrete only one large salivary mass before copulation. Hence, males of *P. cognata* invest in mating without the direct physical interaction of females. This enables us to rule out the confounding effect of direct female influence on the outcome, a shortcoming of previous studies concerning cryptic choice. In most other species, females and males must be allowed to copulate in order to measure male expenditure during mating. Thus, female actions during copulation cannot be controlled for. Due to the mating behaviour of male *P. cognata*, we easily circumvent this problem.

In a previous study we found that sperm is transferred continuously during copulation in *P. cognata* (L. Engqvist and K. P. Sauer, unpublished data) as in other scorpionflies (e.g. Sauer *et al*. 1997, 1998). Consequently, more sperm is transferred in longer copulations. The first aim of this study was to investigate the influence of nuptial gift size on copulation duration. Hence, does the secretion of larger salivary masses result in copulations of longer duration? Second, we examined the effect of male condition on relative male mating effort. Finally, we investigated the possibility of cryptic male choice. In accordance with our hypothesis, males only offer larger salivary masses to females of higher fecundity if the production of a large salivary mass is costly. In contrast, males allocate resources indiscriminately if mating effort is not constrained by available resources.

2. MATERIAL AND METHODS

(a) *Influence of salivary mass size on copulation duration*

We estimated salivary mass size from photographs we took in the time interval between the secretion of the salivary mass and the onset of copulation. We took 30 photographs during the first and second generations in 1998 without any obvious disturbance to pairs since no interruption of copulations occurred after this procedure. All photographs were taken from the same fixed distance (45 mm). The salivary masses that were photographed were all produced by different males.

Slides were projected onto a white wall (distance *ca.* 11 m). The maximum and minimum diameters of salivary masses were measured to the nearest 0.1 mm using callipers. By measuring slides of objects of known length that were taken and projected in the same way, we were able to calibrate all measures to actual lengths. The size of the salivary mass was calculated using the formula of an ellipse, i.e. area $= \text{radius}_{\max} \times \text{radius}_{\min} \times \pi$. We checked mating pairs at least every 10 min. We were always able to determine the exact time at which copulation began and, in most cases, the time of copulation termination. If not, it was calculated by dividing the time elapsed since the last control, which never exceeded 10 min, by a factor of two.

We used F_1 offspring from field-caught adults (near Freiburg im Breisgau, Germany) that were bred using standard breeding protocols (see Sauer 1970, 1977; Thornhill & Sauer 1992). Following emergence, animals were held in two large enclosures (150 cm × 70 cm × 70 cm) containing stinging nettle (*Urtica dioica*) twigs. Each enclosure contained 15 males and 15 females. Animals were supplied with water *ad libitum* and either five or ten one-segment pieces of last-instar mealworms (*Tenebrio molitor*) per enclosure and day.

(b) *Influence of male condition on relative mating effort*

The scorpionflies were treated as in the previous experiment, but males and females were separated until sexual maturity. Sixty males were held in two large enclosures that were provided with either five or ten one-segment pieces of last-instar mealworms per day. Females were held individually in small (8 cm × 3.5 cm) plastic tubes. Females were supplied with water *ad libitum* and a one-segment piece of last-instar mealworm every sixth day. Females are barely able to produce eggs under such a low-nutrient treatment.

Shortly after males had reached sexual maturity (*ca.* ten days of age), mating trials were performed in medium-size enclosures (30 cm × 30 cm × 60 cm). A maximum of six females and six males were placed in each enclosure. Following female attraction, there is usually a long period of premating before males initiate copulation by secreting a salivary mass. Just after salivary mass production, but before the onset of copulation, pairs were interrupted and separated. We collected 34 salivary masses from different males. Males were immediately killed under anaesthesia and transferred to tubes containing 70% ethanol where they were held until preparation. The salivary mass was dried at 90 °C for four days. The dry weight was subsequently measured to the nearest 0.01 mg on days 4–6 after the mating trial. The obtained repeatability of salivary mass dry weight

was high (ANOVA, coefficient of intraclass variation $r_i = 0.990$, $F_{33,65} = 300.5$, $p < 0.0001$). Furthermore, there was no difference in weight between the three measurements (repeated-measures ANOVA, $F_{2,30} = 0.643$, $p > 0.5$). Therefore, we concluded that the salivary masses were completely dried on day 4 and we used the mean value of the three measurements.

In order to evaluate the size of the salivary gland, the abdomen was carefully cut laterally with a fine pair of scissors. This was done soon (< 3 h) after the mating trial. Subsequently, the dissected male was kept another day in 70% ethanol. This procedure hardens the tissue, thereby preventing the salivary gland from rupturing during dissection. Following dissection, the salivary gland was dried for four days. Akin to the salivary masses, dried glands were weighed on days 4–6 following dissection. The repeatability was high (ANOVA, $r_i = 0.996$, $F_{33,59} = 739.7$, $p < 0.0001$) and the weight of the salivary glands did not decrease with time (repeated-measures ANOVA, $F_{2,22} = 0.332$, $p > 0.7$). Consequently, we were able to use the mean value of the three measurements. In order to estimate the dry weight of the salivary gland before copulation, we added the weight of the salivary mass produced to the weight of the dissected salivary gland.

We used the mean length of the left and right forewings as a measure of body size. Measurements were made to the nearest 0.1 mm with a dissecting microscope at ×10 magnification. Males were weighed to the nearest 0.1 mg before every mating trial. We used the residuals from the regression of body size on body weight as an index of condition.

(c) *Influence of female condition on male mating effort*

Males were assigned to one of two treatments. In the high-nutrient treatment, a large enclosure (150 cm × 70 cm × 70 cm) with 30 males was supplied with ten one-segment pieces of last-instar mealworms every day. The males in the low-nutrient treatment were given only five one-segment pieces of last-instar mealworms per enclosure per day. A total of 60 males were used. Females, which in contrast were held individually in small (8 cm × 3.5 cm) plastic tubes, were also assigned to one of two treatments. The females assigned to the good-condition treatment were given a one-segment piece of last-instar mealworms every third day and those in the poor-condition treatment one segment every sixth day. The females in the good-condition treatment were only used if their body weight exceeded 45 mg. Accordingly, the maximum body weight of the females in the poor-condition treatment was set at 40 mg. None of the good-condition females and only one poor-condition female had to be discarded. Our manipulation of female condition resulted in a mean weight difference between the two female treatments of *ca.* 10 mg (good-condition treatment 48.5 ± 0.28 mg, poor-condition treatment 38.0 ± 0.20 mg; $t_{102} = 30.6$, $p < 0.001$), though there was no difference in female size (i.e. wing length) between the two female treatments (good-condition treatment 12.7 ± 0.040 mm, poor-condition treatment 12.7 ± 0.043 mm; $t_{102} = 0.033$, $p > 0.9$). The minimum weight difference between females mated to the same male was 7.2 mg, whereas the maximum difference was 17.1 mg. From previous experiments (L. Engqvist and K. P. Sauer, unpublished data), this handling is known to result in a large significant difference in female fecundity between the female treatments.

Each male was allowed to mate twice, once with a female from the good-condition treatment and once with a female from the poor-condition treatment. Half of the males in each treatment were allowed to mate with a good-condition female first and the other half mated with a poor-condition female first. All matings were interrupted just before the onset of copulations and the weight of the salivary mass was determined as described above. After the first mating, males were supplied with half a segment of a mealworm in order to recover from the mass loss due to the salivary mass secretion. No further feeding occurred afterwards. Mating trials were repeated within six days after the first copulation.

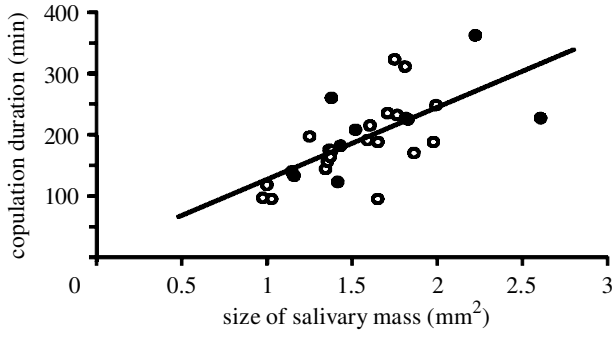

Figure 1. Relationship between the size of the secreted salivary mass and copulation duration. Solid symbols, first generation in 1998; open symbols, second generation in 1998. The line is from the least-squares regression.

As in the previous experiment, we used the residuals from the regression of body size on body weight as an index of condition. We could not measure the body size of two males in the low-nutrient treatment reliably due to worn-out wing tips. Consequently, we do not have an estimate of male condition for these males. Male condition did not differ between matings (repeated-measures ANOVA, $F_{1,49} = 1.89$, $p > 0.15$) and was highly repeatable (ANOVA, $r_i = 0.884$, $F_{49,50} = 16.2$, $p < 0.0001$). Our manipulation resulted in a significant difference in male condition between the two male nutrient treatments (low-nutrient treatment −2.13 ± 0.66 mg, $n = 24$; high-nutrient treatment 1.97 ± 0.73 mg, $n = 26$; $F_{1,48} = 17.2$, $p = 0.0001$).

(d) *Statistical analysis*

We used parametric statistics throughout the analysis and all dependent variables conformed to normality (Lilliefors, $p > 0.2$). Statistical analyses were performed using SPSS 9.0 software. Means are given as means ± s.e. unless specified otherwise.

3. RESULTS

(a) *Influence of salivary mass size on copulation duration*

The mean ± s.d. salivary mass size of our sample was 1.57 ± 0.37 mm^2 ($n = 30$) and the mean ± s.d. copulation duration amounted to 193 ± 66 min ($n = 30$). The size of the salivary mass was positively correlated with copulation duration ($y = 118x + 9.2$ min, $r^2 = 0.435$, $F_{1,28} = 21.6$, $p < 0.001$; figure 1). The intercept of the linear regression did not differ significantly from zero (9.2 ± 40.7 min, $F_{1,28} = 0.05$, $p > 0.8$).

(b) *Influence of male condition on relative mating effort*

We measured the salivary masses and gland weights of 34 males. The mean ± s.d. salivary mass dry weight was 0.857 ± 0.184 mg, whereas the mean ± s.d. estimated

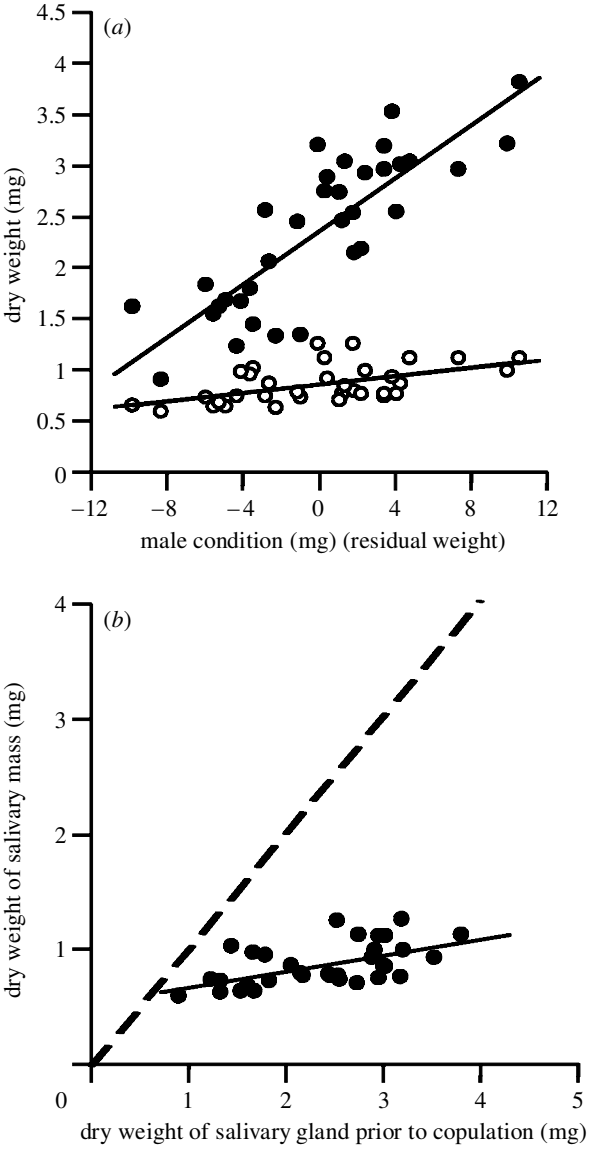

Figure 2. (*a*) Relationship between male condition and estimated dry weight of the salivary gland prior to copulation (solid symbols) and between male condition and dry weight of the secreted salivary mass (open symbols). The lines are from the least-squares regression. (*b*) Relationship between the estimated dry weight of the salivary gland prior to copulation and dry weight of the secreted salivary mass. The solid line is from the least-squares regression. The dashed line indicates the maximum possible male mating effort.

salivary gland dry weight before copulation amounted to 2.36 ± 0.75 mg. We found a significant positive correlation between the size of the salivary mass and male condition ($y = 0.0204x + 0.857$ mg, $r^2 = 0.28$, $F_{1,32} = 12.5$, $p = 0.001$; figure 2*a*). Similarly, with increasing male condition the estimated size of the salivary gland before copulation increased as well ($y = 0.13x + 2.36$ mg, $r^2 = 0.69$, $F_{1,32} = 71.4$, $p < 0.001$; figure 2*a*). However, the slopes differed significantly from each other (salivary gland $b = 0.13 \pm 0.015$, salivary mass $b = 0.0204 \pm 0.0058$; $z = 3.41$, d.f. = 64, $p < 0.001$). This implies that, with increasing size of the salivary gland, males produce larger salivary masses ($y = 0.140x + 0.527$ mg, $r^2 = 0.322$, $F_{1,32} = 15.2$, $p < 0.001$; figure 2*b*), but the slope of the regression line is smaller than unity and the intercept larger than zero (slope $b = 0.140 \pm 0.036$, $t_{33} = 3.90$, $p < 0.001$; intercept $a = 0.527 \pm 0.088$, $t_{33} = 5.96$, $p < 0.001$; figure 2*b*). Accordingly, relative mating investment decreases with increasing male condition and size of salivary gland.

Table 1. *Results of a repeated-measures ANOVA with the dry weight of the salivary mass secreted by the same male for females of different quality as repeated measures*

source of variation	d.f.	mean sum of squares	*F*	*p*
female condition	1	0.0428	3.000	0.089
female condition × male treatment	1	0.1170	8.250	0.006
female condition × mating order	1	0.0371	2.600	0.113
female condition × male treatment × mating order	1	0.0025	0.178	0.675
error	48	0.0142	—	—

(c) *Influence of female condition on male mating effort*

A total of 52 males mated with two females, 26 males from the high-nutrient treatment and 26 males from the low-nutrient treatment. Fourteen out of the 26 low-nutrient males and thirteen out of the high-nutrient males mated with a poor-condition female first. We performed a repeated-measures ANOVA on our data with salivary mass size with respect to female condition treatment as repeated measures and mating order and male treatment as factors (table 1). Overall, female condition had no significant influence on the size of the salivary mass produced by males (poor-condition females 0.775 ± 0.021 mg, good-condition females 0.816 ± 0.020 mg; table 1). However, there was a significant interaction between female condition and male treatment (table 1). Males in the low-nutrient treatment produced a significantly larger salivary mass when mating with high-quality females as compared to matings with low-quality females (poor-condition females 0.734 ± 0.024 mg, good-condition females 0.845 ± 0.026 mg, $t_{25} = 3.51$, $p = 0.002$; figure 3), whereas males in the high-nutrient treatment offered salivary masses of similar weight to both females (poor-condition females 0.815 ± 0.033 mg, good-condition females 0.788 ± 0.029 mg, $t_{25} = 0.76$, $p > 0.4$; figure 3). The difference in weight between the two salivary masses (good-condition female–poor-condition female) produced by one male tended to be larger if the male mated with a low-quality female first (low-nutrient males with a poor-condition female first 0.136 ± 0.044 mg, low-nutrient males with a good-condition female first 0.080 ± 0.045 mg, high-nutrient males with a poor-condition female first 0.021 ± 0.061 mg and high-nutrient males with a good-condition female first −0.074 ± 0.032 mg; table 1). However, this interaction between female quality and mating order was not significant (table 1).

Although our manipulation resulted in a significant difference in male condition between the two male nutrient

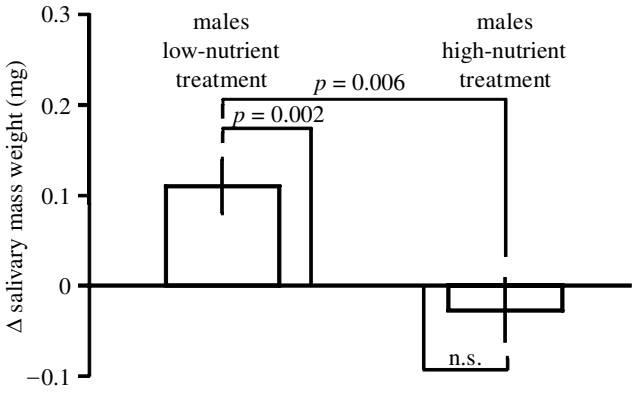

Figure 3. Mean ± s.e. dry weight difference between the salivary masses secreted by one male in matings with good-condition and poor-condition females. A positive value signifies a larger salivary mass in the mating with the high-quality female. The sample size is 26 for both male treatments. n.s., not significant.

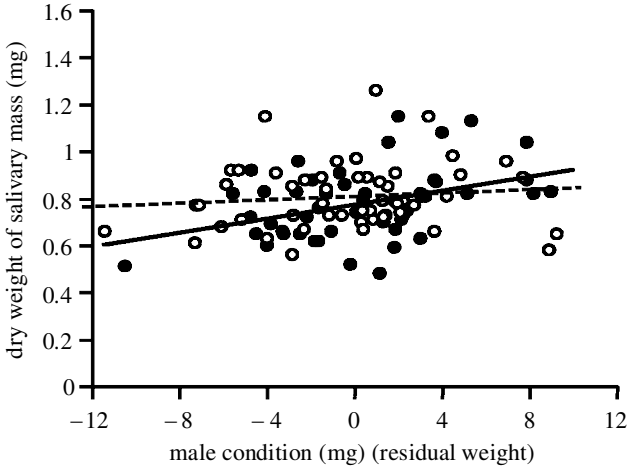

Figure 4. Influence of male condition and female treatment on the dry weight of the secreted salivary mass. Solid symbols, poor-condition females; open symbols, good-condition females. The lines are from least-squares regressions. Solid line, poor-condition females; dashed line, good-condition females.

treatments, the mean salivary mass weight did not differ between treatments (low-nutrient treatment 0.789 ± 0.020 mg, high-nutrient treatment 0.801 ± 0.026 mg; $F_{1,50} = 0.134$, $p > 0.7$). Males in the low-nutrient treatment produced slightly though not significantly larger salivary masses than males in the high-nutrient treatment in copulations with high-quality females (low-nutrient males 0.845 ± 0.026 mg, high-nutrient males 0.788 ± 0.029 mg; $F_{1,50} = 2.09$, $p = 0.15$). Males in the high-nutrient treatment tended to produce larger salivary masses than males in the low-nutrient treatment in matings with low-quality females (low-nutrient males 0.734 ± 0.024 mg, high-nutrient males 0.815 ± 0.033 mg; $F_{1,50} = 3.86$, $p = 0.055$). Since our nutrient manipulation did not divide our sample into two discrete non-overlapping distributions of male condition, we pooled the data from the two male nutrient treatments in order to analyse the influence of male condition on the size of the salivary mass more accurately. Male condition had a significant influence on the size of the salivary mass produced in matings with poor-condition females ($r = 0.40$, $F_{1,48} = 9.1$, $p = 0.004$; figure 4), but not in matings with good-condition females ($r = 0.11$, $F_{1,48} = 0.537$, $p > 0.4$; figure 4). However, these two slopes did not differ significantly from each other (poor-condition females $b = 0.0149 \pm 0.005$, good-condition females $b = 0.0036 \pm 0.005$; $t_{98} = 1.80$, $0.05 < p < 0.1$; figure 4).

4. DISCUSSION

Three major conclusions can be drawn from this study on nuptial gift size in the scorpionfly *P. cognata*. First, the size of the nuptial gift influences copulation duration (figure 1) and, ultimately, the number of sperm transferred. Increasing the size of the salivary mass enables males to transfer more sperm during copulation. Hence, the salivary mass of *P. cognata* functions as mating effort, which of course does not exclude the possibility that it functions as paternal investment as well (Quinn & Sakaluk 1986; Simmons 1995; Reinhold 1999), as has been shown in the scorpionfly *P. vulgaris* (H. Kullmann and K. P. Sauer, unpublished data). Second, the size of the salivary gland increases with increasing male condition (figure 2*a*). Consequently, males in better condition are able to secrete larger salivary masses. However, with increasing salivary gland size, the proportion of the available resources invested in the current mating continuously decreases resulting in relatively lower mating costs for males in good condition (figure 2*a*,*b*). Finally, we demonstrated that males of the scorpionfly *P. cognata* choose cryptically by increasing the size of their salivary mass in matings with high-fecundity females (table 1 and figure 3). In accordance with our hypothesis, male cryptic choice was influenced by relative mating investment: highly investing males were choosy, whereas males making a relatively low mating effort were comparatively indiscriminate (figure 3).

Recently, interest in the theory of optimal sperm allocation and mating effort has increased considerably (Parker 1990; Parker *et al.* 1996, 1997; Fryer *et al.* 1998; Galvani & Johnstone 1998). However, comparatively few empirical studies have investigated the influence of female quality on male mating effort (e.g. Gage & Barnard 1996; Sauer 1996; Gage 1998; Parker *et al.* 1999; Wedell & Cook 1999) and, to the authors' knowledge, none have considered male phenotypic variation. This study further supports the cumulating evidence that female quality influences male mating effort. Fortunately, our results are not confounded by the influence of female quality itself on the outcome, hitherto a problem with virtually all research concerning cryptic choice, cryptic male as well as cryptic female choice. It is, for instance, difficult to determine whether an increase in ejaculate size in copulations with high-quality females is due to cryptic male choice or whether ejaculates are transferred to those females with greater ease (see, for example, Gage 1998). Since males of *P. cognata* secrete their salivary mass without physical interaction from females, we can conclude that the weight difference in the salivary masses produced by males in poor condition for females of high and low fecundity can only be the result of male differential investment and, hence, that it represents an example of cryptic male choice.

The assumption that males discriminate between females, investing more in copulations with females of higher fecundity, is further confirmed by the fact that only males in poor condition discriminate. Obviously, the mating effort of males in good condition is relatively low. At each mating they invest a relatively small fraction of their available resources (figure 2*a*), whereas males in poor condition invest a considerable portion of their limited mating resources. Consequently, the importance of female quality in any single mating will differ between males. For a male in poor condition, cautious resource allocation in matings with low-quality females will pay off since the saved resources can be invested in the next copulation, hopefully with a female of high quality. In contrast, for a male in good condition, prudence in matings with low-quality females will not be advantageous since it will have sufficient resources for future matings anyway.

Why do males in good condition with large salivary glands not increase the size of their secreted salivary mass more than they do? They certainly have enough resources to do so (figure 2*a*). There are several possible explanations for this phenomenon. Males in better condition may be more attractive to females. Consequently, they will have the opportunity of mating more often and they must budget their resources for more successive matings accordingly. At first glance this contradicts our previous argument, i.e. that males in poor condition are more discriminative. However, our findings here support the view that males in poor condition are more cautious concerning the quality of their mating partner in any particular mating since their relative mating effort is higher. Differences in attractiveness and, consequently, in resource allocation across successive matings may be the reason for this phenotypic variation in relative mating effort between males. Another possibility is that males are in some way constrained from increasing the size of their salivary mass, i.e. there is a maximum limit to the size of the salivary mass a male can secrete.

The present study emphasizes the importance of female fecundity on male mating effort in general and in the mating system of *P. cognata* in particular. Males are able to discriminate between females of different fecundity and offer larger salivary masses in matings with high-quality females, an example of cryptic male choice. Moreover, to the authors' knowledge this study provides the first confirmation, at an intraspecific level, that, with increasing relative male mating effort, the strategic allocation of limited resources will be of greater importance. Only males who invest a considerable portion of available resources are sensitive concerning the quality of their female mating partner.

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