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A life-history perspective on strategic mating effort in male scorpionflies

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In species with high male mating effort, there is a trade-off between mating effort spent in a current mating and resources left for future matings. Consequently, to maximize their reproductive success, males have to invest strategically, saving resources in matings with low reproductive gain for future, more valuable matings. However, as males age, the expected future reproductive success constantly declines. Thus, the importance of resource rationing may drastically change during a lifetime. Males of the scorpionfly *Panorpa cognata* offer females a costly nuptial gift before copulation, which functions as male mating effort. Resources for the production of these salivary masses are severely limited for males in poor condition. We found that males invested more in copulations with high-quality females than in copulations with low-quality females. However, males ceased to discriminate as they became older. Old males, with a relative small number of expected future matings, did not invest differentially in copulations with high- versus low-quality females. In copulations with low-quality females, males invested more in late than in initial matings, whereas in matings with high-quality females, time of mating had no influence on mating effort. These results imply that males adaptively change their resource allocation strategy during the course of the season. Initial matings seem to be characterized by male prudence; in later matings, males seem to adopt a more opportunistic mating strategy. *Key words:* mating investment, nuptial gifts, *Panorpa,* resource allocation, scorpionflies, sperm competition, sexual selection. *[Behav Ecol 13:632–636 (2002)]*

Males usually spend less energy and resources than females on parental investment (Trivers, 1972). Consequently, female reproductive success is usually limited by resource availability for offspring production, whereas male reproductive success is mainly limited by access to mates (Bateman, 1948). As a result, males usually spend substantial effort on mate searching and attraction, for example, to obtain fertilization opportunities and sire as many offspring as possible (e.g., Andersson, 1994; Thornhill and Alcock, 1983). Male mating effort (sensu Low, 1978) is expressed in a wide variety of forms. We are all familiar with the courtship songs of birds and various insects (Andersson, 1994). The precopulatory mate guarding of amphipods and isopods (Elwood and Dick, 1990; Jormalainen, 1998) is another example of mating effort by males.

However, male mating effort need not be confined to investment in obtaining matings. In his seminal paper, Parker (1970) explained that male struggle for fertilization continues after copulation in form of sperm competition. Since then, researchers have been aware that males may invest heavily in matings to increase the proportion of offspring sired. Recently, our understanding of male mating effort through ejaculate investment has increased significantly (for review see Birkhead and Møller, 1998). If male fertilization success depends on the number of sperm transferred, the cost of ejaculates may be substantial (e.g., Dewsbury, 1982; Nakatsuru and Kramer, 1982; Olsson et al., 1997), and this will in turn lead to strategic allocation of ejaculates.

Theory predicts that males should decrease investment in matings with decreasing risk of sperm competition (Parker et al., 1997), with increasing number of competing ejaculates (Parker et al., 1996), and with decreasing fecundity of females (Reinhold et al., 2002). These predictions generally have good empirical support (e.g., Engqvist and Sauer, 2001; Gage, 1991; Gage and Barnard, 1996; Sauer et al., 1997; Simmons and Kvarnemo, 1997; Wedell and Cook, 1999). How males should allocate resources for mating effort in a life-history perspective has attracted considerably less interest (but see Candolin, 2000a; Galvani and Johnstone, 1998; McCurdy et al., 2000; Polak and Starmer, 1998; Reinhold et al., 2002; Thomas et al., 1998). At each stage of life history, individuals are expected to maximize reproductive success and behave accordingly (Stearns, 1992). However, a specific behavior, which is adaptive at one time, need not be beneficial at a later stage in life. Withholding resources in matings with low reproductive gain for future, more valuable matings, will only be advantageous if the probability of obtaining these matings is reasonably high. The stochastic nature of male mating success can thus reduce the benefit of saving resources for future matings because a mating may always be the male's last one (Reinhold et al., 2002). Males should be less prone to be choosy and conserve mating resources especially in cases with low future mating success. It has been shown, for instance, that male *Corophium volutator* amphipods, *Drosophila* fruit flies, and milkweed leaf beetles infected by parasites increase mating effort compared to uninfected males (Abbot and Dill, 2001; McCurdy et al., 2000; Polak and Starmer, 1998), and male three-spined sticklebacks with low prospects of survival intensify costly sexual signaling (Candolin, 1999, 2000b). Sticklebacks also increase signaling intensity over their reproductive lifetime (Candolin, 2000a). Similarly, Thomas et al. (1998) found that male choosiness in *Gammarus aequicauda* was reduced when the chance of future mating opportunities decreased. Generally, we expect males to decrease choosiness and increase relative mating effort with decreasing prospects of future matings (Galvani and Johnstone, 1998; Reinhold et al., 2002).

We tested these predictions concerning male mating effort using the scorpionfly *Panorpa cognata* Ramb. At our sample

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site, this scorpionfly has two discrete generations per year. Females are polyandrous, creating high levels of sperm competition. Males invest substantially in matings by offering a nuptial gift. The size of this salivary mass, which males produce before copulation, influences copulation duration (Engqvist and Sauer, 2001) and, consequently, the number of sperm transferred during copulation (Engqvist, 2000). The larger the salivary mass, the more sperm are transferred. In this sense, the salivary mass of *P. cognata* functions as mating effort in correspondence to nuptial gifts in a variety of insect species (for review, see Vahed, 1998).

Consistent with theoretical predictions, we previously demonstrated that males manipulate the size of the produced salivary mass in relation to the quality (i.e., fecundity) of the female. Males with a limited supply of saliva offer high-quality females larger salivary masses than they offer to low-quality females (Engqvist and Sauer, 2001). Thus, males save resources in copulations with low-quality females for future copulations with higher reproductive gain. However, this study (Engqvist and Sauer, 2001) only considered male mating effort early in the mating season. Later the benefit of conserving resources for future matings should decrease because the number of expected future matings constantly declines. Therefore, late in the mating period, we expected males to invest relatively more of the available saliva in each copulation compared to initial matings. Moreover, as the opportunity for future matings decreases, males should invest resources increasingly carelessly. For that reason, we expect the effect of male prudent investment—differential investment in high- versus low-quality females—to diminish late in the mating season. In the present study, we analyzed relative mating effort of *P. cognata* males. We aimed at comparing male prudence of resource allocation early and late in the mating season and measured relative mating effort as the amount of saliva invested in relation to saliva available in the salivary glands.

MATERIALS AND METHODS

We used F_1 offspring from field-caught adults (near Freiburg i. Br., Germany) that were bred using standard breeding protocols (see Sauer, 1970, 1977; Thornhill and Sauer, 1992). After emergence, males were held in enclosures (60 × 30 × 30 cm) containing cut stinging nettle, *Urtica dioica,* stems and leaves. Each enclosure contained 12 males. Animals were supplied with water ad libitum and four one-segment pieces of last-instar mealworms, *Tenebrio molitor,* per enclosure every second day. This corresponds to a low nutrient diet, which is important because a constrained energy allocation to saliva production was a necessary prerequisite for this experiment (cf. Engqvist and Sauer, 2001). All animals were held at 18 ± 1°C, with a 18:6 h light : dark photoperiod.

We measured the mating effort of males once, either early in the mating season (early mating period) or at a later stage in life (late mating period). Males were either mated to a high-quality female or to a low-quality female. Thus, males were randomly assigned to one of four mating situations in a 2 × 2 experimental design. Males in the early mating period were allowed to mate directly after reaching sexual maturity. The mean ± SD age of males at the early mating trial was 12.6 ± 1.8 days (range: 9–16). We allowed males assigned to the late mating period to mate freely for approximately another 20 days. Consequently, the mean ± SD age of males was 31.8 ± 3.4 days (range: 25–37) at the late mating trial. In the time after reaching sexual maturity until this age, male mortality is trivial (in this experiment two out of 75 males), so our two subsamples do not differ with respect to e.g. male viability.

The males tested late were held in identical enclosures and under identical food regime as described above. Six males and six females of both high and low quality were held in each enclosure. Every day, we swapped individuals, females as well as males, between cages, simulating a large, patchily distributed population. We did this to eliminate the random effect due to differences between enclosures. Females used in the mating trials were held individually in small (8 × 3.5 cm) plastic tubes and supplied with water ad libitum and either a one-segment piece of last-instar mealworm every third day (high-quality females) or a one segment piece every sixth day (low-quality females). After adult emergence, females assigned to the late mating period were held on a low nutrient diet at 8°C until 10 days ahead of the mating trials (mean ± SD of time spent in 8°C: 20.1 ± 2.0 days), when they were transferred to 18 ± 1°C. We did this to delay development. For the females used in the late mating trial, mean ± SD time spent at 18 ± 1°C was to 12.2 ± 1.4 days. Consequently, males in the different treatments were paired with females of similar physiological age. Our nutrient manipulation resulted in a significant difference in fecundity between female quality treatments (mean ± SE, high-quality females: 55.7 ± 1.7 eggs; low-quality females: 6.6 ± 1.7 eggs; $t_{84} = 24.3$; $p < .0001$) but not between mating periods (mean ± SE, high-quality females: early mating period 56.4 ± 2.4 eggs; late mating period 54.7 ± 2.4 eggs; $t_{40} = 0.49$; $p > .6$; low-quality females: early mating period 8.5 ± 1.8 eggs; late mating period 4.7 ± 1.3 eggs; $t_{42} = 1.7$; $p = .09$).

All mating trials were performed in enclosures (60 × 30 × 30 cm), in most cases containing six males and either six high-quality or six low-quality females. At the last day of both mating trials, one cage from each treatment contained only five males and females because there were not enough males to fill the last cage. We used virgin females only. Just after salivary mass production but before the onset of copulation, pairs were interrupted and separated. Males were immediately killed under anesthesia and transferred to tubes containing 70% ethanol, where they were held until preparation. The preparation of salivary glands followed standard protocols (Engqvist and Sauer, 2001). The salivary glands and salivary masses were dried at 90°C for 4 days. We subsequently measured the dry weight to the nearest 0.01 mg on days 4, 5, and 6 after the mating trial. The obtained repeatability of salivary mass dry weight was high (ANOVA, coefficient of intraclass variation: $r_i = .981$; $F_{128,254} = 154.2$; $p < .0001$). Furthermore, there was no difference in weight between the three measurements (repeated-measures ANOVA: $F_{2,124} = 0.565$; $p > .5$). Likewise, for the measurement of salivary gland, dry weight was highly repeatable (ANOVA: $r_i = .993$; $F_{128,239} = 383.0$; $p < .0001$), and the weight of the salivary glands did not decrease with time (repeated-measures ANOVA: $F_{2,114} = 1.17$; $p > .3$). Therefore, we concluded that the salivary masses and glands were completely dried on the fourth day, and we used the mean value of the three measurements. To estimate the dry weight of the salivary gland before copulation, we added the weight of the produced salivary mass to the weight of the dissected salivary gland.

The salivary mass dry weight conformed to normality (Lilliefors, $p > .2$). The size of the produced salivary mass is largely influenced by the size of the male's salivary gland. We therefore used ANCOVA throughout the analyses, with salivary gland size as the covariate to control for this effect, enabling us to compare relative mating effort. Between groups, the regression coefficients from the regression of salivary gland size on salivary mass size were not significantly different from each other (Tukey-Kramer; $p > .1$). On four occasions, we recorded salivary masses from two males in the same mating trial (two pair of males mating with low-quality females in the late mating trial, and from the early mating trial, one pair of males mating with high-quality females and one mating with low-

Table 1
ANCOVA of the effects of female quality and time of mating on the size of the produced salivary mass

Source of variation	df	Mean SS	F	p
Size of salivary gland	1	194×10^{-3}	17.2	<.001
Time of mating	1	2.34×10^{-3}	0.20	>.6
Female quality	1	66.9×10^{-3}	5.93	<.05
Time of mating × Female quality	1	60.7×10^{-3}	5.38	<.05
Error	78	11.3×10^{-3}		

Salivary gland size is used as the covariate.

quality females). To present independent observations, we used the mean values of salivary mass and gland size taken from two males in the same mating trial. Statistical analyses were performed using SPSS 9.0 and JMP 3.2.2.

RESULTS

We measured mating effort of 47 males early in the mating season. Of these, 25 mated with a high-quality female and 22 with a low-quality female. Late in the mating season, we collected data from 40 matings: 18 with high-quality females and 22 with low-quality females. Mean ± SD dry weight of the salivary glands in our total sample was 1.524 ± 0.433 mg, and the mean ± SD salivary mass dry weight was 0.708 ± 0.118 mg. Salivary gland size did not differ between early and late mating males (mean ± SE, early mating period: 1.517 ± 0.066 mg; late mating period: 1.532 ± 0.069 mg; $F_{1,81} = 0.03$; $p > .8$). The size of the salivary gland had a significant influence on the size of the produced salivary mass ($y = 0.089x + 0.572$ mg; $R = .327$; $F_{1,81} = 9.69$; $p = .003$). When controlling for the size of the salivary gland, we found that males offered high-quality females significantly larger salivary masses than low-quality females, whereas time of mating had no significant effect on male mating effort (Table 1). There was, however, a significant interaction between female quality and time of mating (Table 1). This significant interaction implies that the effect of female quality was different in the early mating period compared to late in the mating season. Early in the mating season males produced significantly larger salivary masses in copulations with high-quality females than in copulations with low-quality females (ANCOVA, female quality: $F_{1,42} = 9.74$; $p = .003$; covariate salivary gland: $F_{1,42} = 8.24$; $p = .006$; Figure 1a). In late matings, there was no difference in salivary mass size between females of different quality (ANCOVA, female quality: $F_{1,35} = 0.04$; $p > .8$; covariate salivary gland: $F_{1,35} = 9.06$; $p = .005$; Figure 1b). This results from an increase in salivary mass size in copulations with low-quality females in the late mating period compared to low-quality females in matings earlier on (ANCOVA, time of mating: $F_{1,38} = 5.99$; $p = .019$; covariate salivary gland: $F_{1,38} = 8.23$; $p = .007$; Figure 2a). In contrast, mating effort in copulations with high-quality females was equally high in both mating periods (ANCOVA, time of mating: $F_{1,39} = 1.61$; $p > .2$; covariate salivary gland: $F_{1,40} = 12.2$; $p = .001$; Figure 2b).

To assure that the different effect of female quality on mating effort in the early and late mating trial was not an effect of delaying female development, which could have changed female behavior, we performed a control experiment. In this experiment female development was delayed as in the previous experiment. To be able to measure male mating effort of young males in copulations with these females, we delayed male development in the same manner. If female behavior change is an effect of the treatment, this change in behavior should also be reflected in this control experiment. We measured the mating effort of 42 males in the control: 23 in matings with high-quality females and 19 in matings with low-quality females. The mean ± SD salivary gland and mass size of this sample was 1.746 ± 0.608 and 0.908 ± 0.183 mg, respectively, which was somewhat higher than in the previous experiment. However, as in the early mating trial of the previous experiment, we found an effect of female quality on male mating effort (ANCOVA, female quality: $F_{1,39} = 8.67$; $p = .005$; covariate salivary gland: $F_{1,39} = 33.6$; $p < .001$). Furthermore, the effect size, measured as the difference in salivary mass size between female treatments when controlling for salivary gland size, was of similar magnitude (control:

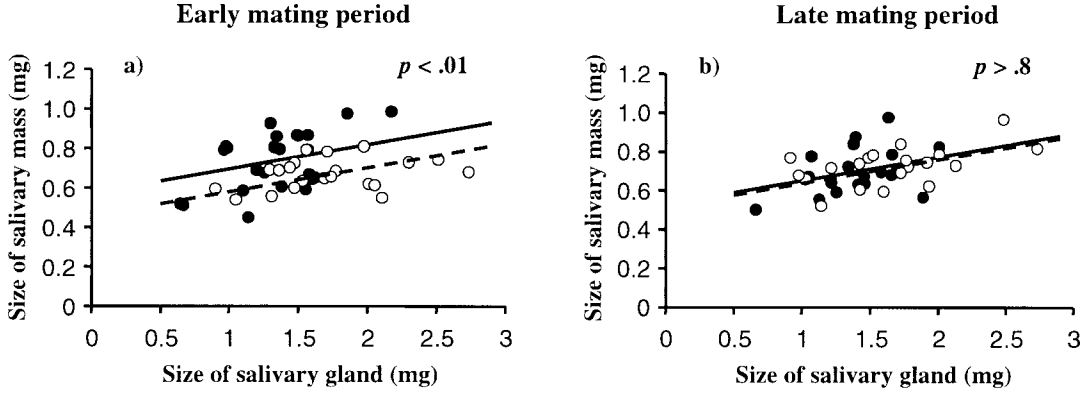

Figure 1
Comparison of relative male mating effort in matings with high- and low-quality females (a) early and (b) late in the breeding season. Solid symbols and lines depict matings with high-quality females, and open symbols and dashed lines depict matings with low-quality females. Lines were calculated using the common pooled regression coefficient, estimated from ANCOVA.

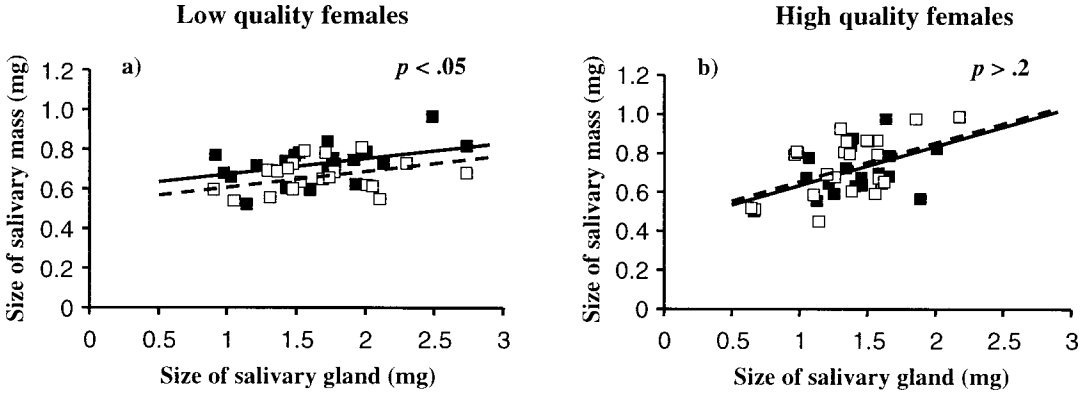

Figure 2
Comparison of relative male mating effort early and late in the breeding season in matings with (a) low-quality females and (b) high-quality females. Solid symbols and lines depict early matings, and open symbols and dashed lines depict late matings. Lines were calculated using the common pooled regression coefficient, estimated from ANCOVA.

0.123 ± 0.042 mg; early mating period: 0.116 ± 0.037; ANCOVA, female quality × experiment interaction: $F_{1,82} = 0.10$; $p > .7$). Thus, it is implausible that the lack of an effect in female quality in the late mating period was caused by a change in female behavior resulting from development delay.

DISCUSSION

The central finding of this study is that male *P. cognata* shift investment strategy during the course of the mating season. Males initially adopt a discriminatory mating strategy, saving resources in matings with low-quality females for future more valuable matings. Later, as the advantage of resource rationing decreases, males become less sensitive to female quality. Thus, previous studies demonstrating differential male mating investment in copulations with high- versus low-quality females in initial matings (Engqvist and Sauer, 2001) are confirmed (Figure 1a). However, as the mating season proceeds, there is a significant change in male discriminatory mating behavior. Late in the mating season, males do not invest differentially (Figure 1b) but spend an equal amount of resources in all matings, regardless of female quality. This results from an increase in relative mating effort later in the mating season in copulations with low-quality females (Figure 2a). In matings with high-quality females, where males already invest heavily in initial matings, no increase in relative mating effort was found (Figure 2b).

Decreasing significance of female quality to male mating effort as the breeding season proceeds is consistent with predictions from theoretical models (Galvani and Johnstone, 1998; Reinhold et al., 2002). However, these models predict a much larger increase in relative mating effort with increasing male age than we found. At the end of the breeding season, one would expect that males invest all resources, saving nothing for the future. In contrast, we found that even in the late mating season, *P. cognata* males seldom produced salivary masses larger than 1.0 mg dry weight, even though the available resources would have been sufficient for gifts of 2.5 mg (cf. Figure 1b). Maximum gift size thus corresponds to approximately 40% of available resources only. Males may still have deliberately conserved some resources because we did not measure mating effort at the absolute end of the breeding season. However, at the time of the second mating trial, male age was considerable, and we therefore doubt that it is advantageous to save 60% of the mating resources for possible future matings. From observations of populations in seminatural conditions (Engqvist, 2000), we know that even at the very end of the breeding season, males never produce salivary masses exceptionally larger than in this study, although males in such experiments often were in considerably better condition. Presumably, salivary mass size is constrained by factors other than the amount of saliva available. The labial glands of males in good condition extend over a major part of thorax and abdomen. Possibly, males are only able to secrete a limited amount of this saliva through the mouth at each time, so that only males with minimal salivary glands are able to exhaust resources (Figures 1 and 2; cf. Engqvist and Sauer, 2001).

Because relative mating effort in matings with low-quality females increased later in the breeding season and there was no significant change for high-quality females, one would also expect mean mating effort to increase over time. In contrast, our analysis did not show a significant effect of time of mating on mean relative mating effort. There are two different alternatives that would account for this result. Either relative mating effort does increase and a larger sample size is needed to reveal this effect, or mean relative mating effort really does not change, but males decrease effort in matings with high-quality females somewhat later in the breeding season. We cannot disentangle these possible effects with the given data.

In the present study, we used only virgin females to keep conditions similar for all males. Late in the breeding season, males may not frequently encounter virgin females, but it is not an implausible event. In the seminatural breeding situation at our laboratory, adults emerge for at least 4 weeks from the end of April until the end of May (Engqvist and Sauer, unpublished data). Consequently, for males emerging early, the chance to associate with a virgin female 30 days later (the mean age of males in the late mating period of this study) is not unlikely.

The adaptive change in male mating effort in relation to expected future mating success has received relatively little attention. Candolin (1999, 2000b) found that male three-spined sticklebacks in poor condition, with low prospects of survival, exaggerate sexual signaling and that signaling intensity is higher in late breeding cycles (Candolin, 2000a). Parasite infection, which lowers the chances of survival, has also been demonstrated to increase male mating effort (Abbot and Dill, 2001; McCurdy et al., 2000; Polak and Starmer, 1998). In close accordance with the present study on scorpionflies, Thomas et al. (1998) found that male choosiness in an amphipod was influenced by the prospects of future mating opportunities. Males closer to the time of moult, when males cannot copulate, changed their discriminating strategy and paired with any female available. In addition to the signifi-

cance of female quality on male mating effort, our results highlight the importance of considering the life-history components of optimal mating effort.

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