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Male attractiveness is negatively genetically associated with investment in copulations

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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. Males are therefore expected to allocate resources prudently across successive matings. Attractive males that will have a high mating success might therefore be forced to decrease mating investment in comparison with less-attractive males. Furthermore, if there is genetic variation in attractiveness, one might expect to find a negative genetic correlation between attractiveness and mating investment. Here, this genetic prediction is tested using the scorpionfly *Panorpa cognata* (Insecta: Mecoptera). In this species, males offer costly salivary secretions as nuptial gifts to females. By producing large secretions, males increase copulation duration and sperm transfer, thus gaining an advantage in sperm competition. I used a full-sib breeding design and found that both attractiveness and mating investment showed considerable heritability. Most importantly, there was a significant negative genetic correlation between attractiveness and mating investment: In families with attractive individuals, males produced smaller salivary secretions than in those with less-attractive males. The results thus demonstrate an important evolutionary trade-off between mating success and sperm competition success. *Key words:* alternative mating strategies, life-history trade-offs, nuptial gifts, *Panorpa*, sexual selection, sperm competition\body. *[Behav Ecol]*

Evolution of polyandry drastically alters the demands on many aspects of male reproduction (see reviews in Birkhead and Møller 1998; Birkhead et al. 2009). Male reproductive success will not only be affected by males' access to female mating partners but also by the success of their sperm in the subsequent competition for fertilizations (Parker 1970; Eberhard 1996; Birkhead and Møller 1998; Simmons 2001). Thus, both pre- and postcopulatory episodes of sexual selection will influence the evolution of male reproductive traits. Nevertheless, the relationship between these elements remains to be resolved (Andersson and Simmons 2006; Hosken et al. 2008). Do males with a higher mating success also enjoy a higher fertilization success per mating? In some species, this is indeed the case (Lewis and Austad 1994; Bangham et al. 2002; Evans et al. 2003; Hosken et al. 2008), whereas the opposite has been found in other species (Warner et al. 1995; Danielsson 2001; Fu et al. 2001; Preston et al. 2001).

A related question concerns the relationship between male investment in pre-and postcopulatory traits. From a life-history resource allocation perspective, one would expect a trade-off between investment in pre- and postcopulatory traits (Parker 1998). For instance, by investing in attractive ornaments, fewer resources will be available for investments in traits increasing postcopulatory reproductive success (see also Simmons and Emlen 2006; Evans 2010; Simmons et al. 2010). Furthermore, if males invest heavily in matings in order to increase fertilization success, resources will be limited for future matings. Attractive males that will have a high mating success might therefore be forced to decrease mating investment in comparison with less-attractive males that might afford to increase mating investment (Simmons 1995; Bussière 2002; Bussière et al. 2005). Thus, the strength of the trade-off between pre- and postcopulatory trait investment will become even more acute because attractive males have to allocate their resources over more matings. A similar conclusion was made in a recent theoretical analyses (Tazzyman et al. 2009), which demonstrated that males with a lower cost of achieving mates (attractive males) should invest less in ejaculates per mating. From these considerations, an important genetic prediction can be inferred (see also Evans 2010; Simmons et al. 2010): If there is genetic variability for male attractiveness, genetic variability in mating investment is also predicted with negative genetic covariation between attractiveness and mating investment.

In this study, I investigate the relationship between mating success and investment in a trait affecting fertilization success in the scorpionfly *Panorpa cognata*. In this species, males invest substantially in matings by the offering of a nuptial gift, a salivary secretion, which is produced prior to the onset of copulation (Engqvist and Sauer 2003b). The salivary mass is consumed by the female during mating, and its size influences copulation duration (Engqvist and Sauer 2001) and, consequently, the number of sperm transferred during copulation (Engqvist and Sauer 2003a). As the sperm competition mechanism largely conforms to a fair raffle (see Parker 1990) of sperm (Engqvist et al. 2007), the size of the salivary mass represents an easy quantifiable male reproductive trait that influences male fertilization success. By producing larger nuptial gifts, males will be more successful in sperm competition. But, as resources are limited, this might come at a cost of a reduced number of potential future matings. The amount of saliva in the salivary glands is highly limited, and there is a high male cost of mating. By comparing typical salivary gland and secretion size (for instance Engqvist and Sauer 2001), it can be estimated that males usually have resources for 1–4 matings

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immediately available before they have to refuel their reserves (see also Engels and Sauer 2006). Males that have a shorter expected time interval between matings (i.e., attractive males) therefore might have to allocate their resources more carefully.

The main objective of this study was to investigate both the phenotypic and genotypic relationship between attractiveness and mating investment. How does male attractiveness and thus expected lifetime mating success affect their investment in matings measured as the amount of saliva offered? Are male attractiveness and salivary mass size heritable? And if so, what is the nature of the genetic correlation between these traits?

MATERIALS AND METHODS

A full-sib design was used. Individuals of the parental generation were all F_1 offspring from animals caught near Freiburg im Breisgau in south-western Germany. Parents were bred on a 12:12 h light:dark photoperiod, which induces diapause development (for details of breeding protocols, see Sauer 1977; Thornhill and Sauer 1992; Engqvist and Sauer 2001). Following emergence, unrelated females and males were randomly paired and put into transparent mating boxes (10 × 10 × 7 cm) containing moist filter paper. Boxes were inspected daily for laid eggs, which were transferred to a new Petri dish containing moist tissue paper. Larvae of the experimental F_2 generation were kept individually in small plastic Petri dishes (Ø5.2 cm) containing moist filter paper at 18 °C on a 18:6 h light:dark photoperiod enabling diapause-free development. They were fed on a diet consisting of a mixture of freeze-dried mosquito larvae (Astra Aquaria, 12 mg every third day) and mealworm (*Tenebrio molitor*) segments (one segment every third day). Fourth instar larvae were transferred to peat-filled cylinders (Ø3.5 cm, peat depth ca. 5 cm), where they entered the pupal stage and finally emerged.

Following emergence, adults were kept on a standardized diet consisting of one mealworm segment every third day. This is plentiful enough to avoid male starvation or fatigue, yet limits its allocation to the salivary gland (Engqvist and Sauer 2001; Engels and Sauer 2006). All adults were held individually in small (8 × 3.5 cm) plastic tubes and supplied with water ad libitum. To determine male salivary mass size, standardized mating trials were performed (Engqvist 2007a) with one female in transparent plastic boxes (10 × 10 × 7 cm) containing moist filter paper and a piece of stem and leaf from a nettle plant (*Urtica dioica*). This was done when males had reached the age of 14 days. Trial females were randomly chosen from a stock that had been bred under similar conditions as described above for the parent generation. Because female weight has an influence on mating investment in *P. cognata* (Engqvist and Sauer 2001, 2002), only females with body weights ranging from 47.5 to 52.5 mg were chosen for the mating trials. Within this range, female weight has a negligible effect (Engqvist 2007a). If no salivary mass was produced, the mating trial was repeated on 2 consecutive days with a different female until a salivary mass was produced. Otherwise, the male was discarded from the analysis. Mating investment was measured as the dry weight of the offered salivary mass. Just after salivary mass production but before the onset of copulation, pairs were interrupted and separated. The dry weight of the produced salivary mass was measured to the nearest 0.001 mg as described in Engqvist and Sauer (2001).

Attractiveness measurements were done on the 12th and 13th day following male emergence (thus on the days preceding the mating investment scorings). These trials were performed in identical boxes with females from the same stock as described above. Like most scorpionflies, *P. cognata* males attract females by emitting a volatile sex pheromone (Thornhill 1979; Kock et al. 2007). The index of male attractiveness was based on the mean duration until males were approached by females, which is a reliable predictor of male lifetime mating success (Engqvist 2000). Female attraction was scored as definite when females were standing closer than 5 mm to the male. Males then almost invariably stop "calling" by reverting the pheromonal gland and instead commence their typical courtship movements (Engqvist and Sauer 2003b; Engqvist 2009). Prior to statistical analysis, attractiveness values were log-transformed and subsequently *z*-transformed. Hence, the attractiveness score is expressed as a standard normal deviate and gives the estimated attractiveness in relation to individuals of average attractiveness. Finally, I took the negative of these values so that positive values correspond to higher than average attractiveness (short duration until female approach) and negative values correspond to lower attractiveness.

Statistical analysis

All analyses were performed with R 2.9.1 (R Development Core Team 2009). Variance and covariance parameters were estimated by restricted maximum likelihood (see Lynch and Walsh 1998) using the *lme* function of the *nlme* library (Pinheiro and Bates 2000). The genetic correlations between traitsr_g, were computed as

$$r_g = \frac{\mathrm{COV}(x,y)}{\sqrt{\mathrm{VAR}(x)\cdot\mathrm{VAR}(y)}},$$

where COV and VAR are the genetic components of covariance and variance of traits *x* and *y* (Falconer and Mackay 1996; Roff 1997). Heritability was estimated as the within-family variation divided by total phenotypic variation (Falconer and Mackay 1996; Roff 1997). It should be noted that estimates based on full-sib analyses must be interpreted with caution as they include both dominance and maternal effects (Roff 1997). However, as individuals were bred individually, common environmental effects can be excluded. Due to relatively small and unbalanced family sizes, I used a jackknife approach to estimate standard errors of the heritability and genetic correlation estimates (Roff and Preziosi 1994; Simons and Roff 1994) and permutation tests (Good 2005) to test their statistical significance. The standard major axis regression used to illustrate the results (see Figure 1) was calculated using the program Model II regression (Legendre P and Legendre L 2001; available from http://www.bio.umontreal.ca/casgrain/en/labo/model-ii.html).

RESULTS

I measured the attractiveness of 122 males from 24 full-sib families. From 90 of these, I was also able to measure the mating investment in their first copulation, measured as the size of the offered salivary mass. The time until female approach, which was used as an index of male attractiveness, ranged between 3 and 360 min with a median of 22 min (quartiles: 7 and 66 min), whereas the mean ± standard deviation dry weight of the salivary mass size was 0.74 ± 0.22 mg.

Both attractiveness and salivary mass size showed large and statistically significant heritable variation (attractiveness: $h^2 = 0.436 \pm 0.206$, permutation test: 10 000 simulations, $P = 0.0015$ and salivary mass size: $h^2 = 0.569 \pm 0.328$, permutation test: 10 000 simulations, $P = 0.0033$). However, as these estimates are based on full-sib analyses, they should rather be considered as upper limits of true heritability. Attractive males produced smaller salivary masses evident from

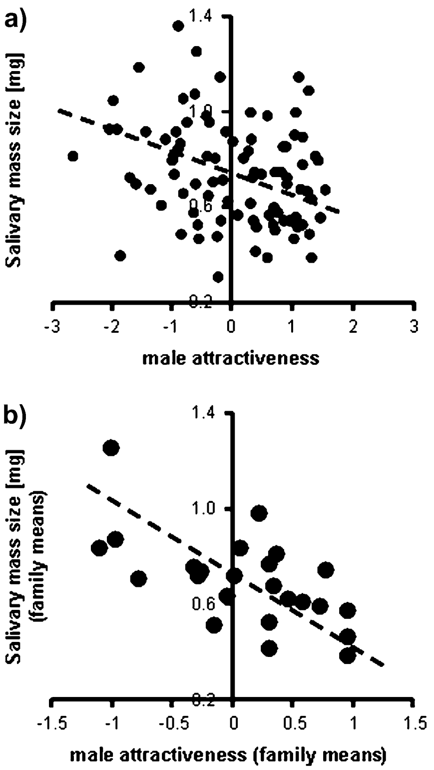

Figure 1
(a) Phenotypic and (b) genetic correlation between male attractiveness and mating investment measured as salivary mass size. The lines indicate the standard major axis (SMA) regressions.

a significant phenotypic correlation between attractiveness and salivary mass size ($r_p = -0.234 \pm 0.104$; $N = 91$, $P = 0.026$; Figure 1a). Furthermore, there was a significantly negative genetic correlation between attractiveness and salivary mass size ($r_g = -0.496 \pm 0.197$, permutation test: 100 000 simulations, $P = 0.031$; Figure 1b). Visual inspection of the data revealed one potentially influential outlier. Excluding this family did not change the results quantitatively or qualitatively ($r_g = -0.509 \pm 0.198$, permutation test: 100 000 simulations, $P = 0.032$)

DISCUSSION

The results clearly show that attractive male scorpionflies invest a smaller amount of their costly saliva secretions in each mating compared with less-attractive males. Furthermore, there is genetic variation for attractiveness, and this genetic variation is manifested in mating investment as well, which is evident from a negative genetic correlation between these 2 traits. Thus, these findings demonstrate both 1) standing genetic variation in life-history resource allocation that influences different components of male reproductive success and 2) a predicted evolutionary trade-off (Parker 1998; Simmons and Emlen 2006) between mating success and sperm competition success.

Since the realization that male reproductive success is influenced also by sperm competition success and cryptic female choice, a number of studies have aimed to study the relation between pre- and postcopulatory sexual selection in more detail. The results of these studies are somewhat ambiguous, and no clear picture has emerged yet. Males with higher mating success can also have higher fertilization success (Lewis and Austad 1994; Bangham et al. 2002; Evans et al. 2003; Hosken et al. 2008). But in other species, higher fertilization success is associated with low mating success (Warner et al. 1995; Danielsson 2001; Fu et al. 2001; Preston et al. 2001; Demary and Lewis 2007). Thus, there seem to be no clear-cut prediction on the association between pre- and postcopulatory male reproductive success. Instead, the processes involved in shaping these patterns need to be disentangled. There are at least 3 different underlying mechanisms shaping the relationship between male mating and paternity success: First, a positive association between pre- and postcopulatory male reproductive success will be expected if females cryptically bias male fertilization success in favor of attractive males (Pizzari et al. 2002; Evans et al. 2003; Pilastro et al. 2004; Safran et al. 2005). Second, there is likely to be an allocation trade-off between investment in pre- and postcopulatory traits. This can lead to a negative relation between mating and fertilization success if males that invest massively in an attractive trait will have to reduce investment in postcopulatory traits and vice versa (Simmons and Emlen 2006; Evans 2010; Simmons et al. 2010). However, the variation in allocation strategies to pre- versus postcopulatory traits can be relatively low in relation to the variation in male resources (see van Noordwijk and de Jong 1986). In this case, males in good condition might afford to invest both in attractiveness and in sperm competitiveness. Finally, there will be trade-off between investment in present versus future matings, and this will affect attractive males more strongly. Irrespective on how much resources males have invested in different traits, attractive males will have a high mating success and will be forced to decrease investment per mating, resulting in reduced sperm competitiveness and fertilization success (see Preston et al. 2001).

Here, my focus has been on this last issue: How attractiveness and increased mating opportunities will shape males' allocation of mating resources to sperm competition. The presented results are very similar to predictions from a theoretical model dealing with nuptial gift size in courtship feeding animals (Bussière 2002). This analysis showed that it will be advantageous for preferred males to reduce gift size because they will encounter more receptive females. A similar but more general conclusion was also made more recently by Tazzyman et al. (2009) showing that attractive males that have a lower cost to achieve matings should invest less per mating. Yet, few studies have investigated the consequences of elevated male mating success on investment per mating. An elegant study where mating success was experimentally manipulated showed that male bushcrickets (*Requena verticalis*) that mate more often invest less per mating (Simmons 1995). Furthermore, asymmetrical males, which presumably have a lower mating success, invest more in matings compared with those anticipating a higher mating success (Simmons et al. 1999). Another study in the tree cricket, *Oecanthus nigricornis*, showed that males with a higher expected mating success adaptively adjust their allocation to nuptial gifts and donated smaller gifts than those with fewer mating opportunities (Bussière et al. 2005). Related to this are studies that show that male changes in social status with a resulting change in mating success are accompanied by changes in sperm characteristic and competitiveness (Froman et al. 2002; Rudolfsen et al. 2006).

In some insect species in which males present nuptial gifts, there is evidence that females prefer males offering large gifts (Lehmann GUC and Lehmann AW 2008). This might be expected if females gain direct nutritional benefits from nuptial gift consumption (Price et al. 1993; Møller and Jennions 2001). However, attractive males might not be the best providers as exemplified here. In order to maintain high mating rate, they must reduce gift or ejaculate size (Bussière 2002). Thus, there might be a conflict resulting from female preferences and male strategic investment. This kind of sexual conflict regarding ejaculate size has been demonstrated in the bluehead wrasse, *Thalassoma bifasciatum*. Here, mating success is highly skewed toward a few males, which consequently release fewer sperm per mating resulting in a reduction in egg fertilization rate (Warner et al. 1995). Potentially, this cost for females mating with males with the highest mating success can thus influence the selection on female mate preferences (van Doorn et al. 2004; Cotar et al. 2008; Härdling et al. 2008). Because female scorpionflies that mate with attractive males receive smaller gifts, this sexual conflict might also be present here. However, it is probably not very important as the nutritional benefit from gift consumption is rather small (Engqvist 2007b). Furthermore, because females in this scorpionfly species are polyandrous, it is arguable whether these direct benefit arguments are relevant. Indeed, discriminating against males giving smaller gifts seems disadvantageous as females can collect gifts from many males.

This study also demonstrated heritability of attractiveness. Although heritability of male traits preferred by females is well established (Andersson 1994), studies demonstrating heritability of attractiveness per se are still quite scarce (Bakker 1993; Wedell and Tregenza 1999; Brooks 2000; Taylor et al. 2007). Here. the heritability estimate was based on a full-sib breeding design. The results therefore do not explicitly show that attractive fathers sire attractive sons, an important assumption in many models of sexual selection (Kokko et al. 2006). Nevertheless, scorpionflies were raised individually, and thus, common environmental effects can be excluded. The results therefore do show genetic variation in attractiveness, but it must not necessarily be inherited from father to son (i.e., dominance effects, mitochondrial or X-chromosomal inheritance, etc.). Increased attractiveness was accompanied by a decrease in mating investment. The results therefore imply heritable variation of alternative mating strategies. Genetic polymorphism associated with alternative mating strategies have been demonstrated in a few species only (Shuster and Wade 1991; Ryan et al. 1992; Lank et al. 1995; Sinervo and Lively 1996; Hurtado-Gonzales and Uy 2009; Evans 2010), yet might have been overlooked if variation is continuous, as in the present study, rather than discrete. Future studies in this direction will help resolving the association between pre- and postcopulatory sexual selection.

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