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Mating behaviour and sexual size dimorphism in *Scathophaga inquinata*

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In the dung fly, *Scathophaga inquinata,* females oviposit on fresh cow droppings where males arrive to mate with females before oviposition. While searching for females, single males spent most of their time in the vicinity of droppings, and were frequently involved in fights with conspecifics. On the dropping, both single males and pairs were attacked by the yellow dung fly, *Scathophaga stercoraria,* and hardly ever by conspecifics. Copulating males were larger than searching males, suggesting selection for large male size. Nevertheless, females were the larger sex. Only a few pairs formed at the dropping; most pairs flew to it. In copulating pairs, females were the flying individual. This was shown in an experiment where copulating pairs were tested for their ability to fly. In addition, pairs were size assortatively mated. Sexual size dimorphism in *S. inquinata* is discussed in relation to the mating behaviour and sexual selection on male and female size. It is suggested that loading constraints may be among the factors that maintain female-biased sexual dimorphism in this species.

1. Introduction

In species with resource-defence polygyny, males fight for access to the resources used by females, and during the aggressive interactions some males are excluded from the best mating areas (Thornhill & Alcock 1983). In such mating systems, the advantage of large body size is expected on theoretical grounds (see Maynard Smith 1982), and a higher mating success of large males has also been shown in many species (e.g. Borgia 1980, McCauley 1982, Otronen 1984, Thornhill & Alcock 1983: table 9.1). Large male mating advantage may also result from female preference for large males (e.g. Simmons 1985). Although large male mating advantage may vary in space and time, and small males may use alternative mating tactics (Thornhill & Alcock 1983), selection on large male size is often strong in resource-defence mating systems.

The dung fly, *Scathophaga inquinata,* is found at cow droppings in covered habitats such as small woodlands. The species is a close relative of the yellow dung fly, *Scathophaga stercoraria*. In the yellow dung fly, males gather at fresh droppings where, due to male-biased sex ratio, competition for females is intensive (Parker 1970, Parker 1978). In the yellow dung fly, large males enjoy higher short-term mating success (Borgia 1980) and males are the larger sex (Otronen 1993). Given the similarity in resource use, similar mating behaviour and trends in size might be expected in *S. inquinata*.

In this paper, I examine the mating behaviour of *S. inquinata* and, in particular, the importance of individual size in the mating system. I observed single males and pairs at fresh cow droppings and recorded male fights and mate searching behaviour. To compare individuals' size, I collected single males and pairs from droppings and from the surrounding vegetation. I also carried out an experiment which shows that females fly and carry the male during copulation.

2. Material and methods

Flies were observed at the end of May 1995, in a small woodland in Southern Finland. The woodland was used by grazing cattle on their way to pastures, and thus, fresh droppings were available there at least twice a day.

2.1. Temporal distribution of flies

Fresh cow droppings of standard size (26 cm in diameter) were placed in the wood at least 5 m apart from each other. Counting was performed on three days, at 3 to 4 droppings per day. The number of searching males and pairs in *S. inquinata* and single males in *S. stercoraria* on the dropping were counted every half hour during the first 2.5 hours (n = 10 droppings) and every hour during the next three hours (n = 4; except 3.5 h, where n = 1).

2.2. Behavioural observations

I observed flies by sitting about 1 m away from fresh cow droppings. I chose the observed pairs or individuals randomly by first choosing "a landmark" on the dropping or in the vegetation and then observing the first individual or pair that came within a couple of centimetres from it. I did not mark the observed individuals and, therefore, only two individuals or pairs were observed at the same dropping to avoid observing the same individuals more than once. In single males, searching on the dropping or in the surrounding vegetation, I recorded the number of times they were attacked, the number of times they attacked other flies, and whether the attacker or the target was conspecific or belonged to the yellow dung fly. I also recorded attacks against pairs and the result (escape or separation of the pair or takeover). Males and pairs were observed for three minutes. Males searching on the dropping were observed for a shorter time because their visits were shorter. Altogether, I spent 20 h observing various components of the mating behaviour.

2.3. Size measurements

Searching males at 7 droppings were collected with a sweep net at 1-hour-old droppings (n = 225). At each dropping, I made 15 sweeps over a circular area about 1 m around the dropping. All searching males on 6 droppings (n = 34), and all pairs on another 7 droppings (n = 128) were captured by placing a plastic tube above them. Individuals were preserved in alcohol and their wing length was measured under a microscope.

2.4. Flight in copula and loading constraints

To find out which sex flies during copula, I collected males and females from the field. I anesthetized half of the males and females with CO_2 and cut one wing off. I left the outermost edge of the wing on in females because males hold their legs around female wings in copula. Then I randomly paired the individuals with a manipulated wing with normal individuals. After 2–5 min copulation in a tube, I opened the tube holding it about 1 m above the floor. The room was dark, except for the light coming from the window about 4 m away from me. After the pair came out, I pushed it gently off the tube edge. The pairs either readily flew towards the window or landed on the floor. Pairs that landed on the floor were pushed gently to see if they could lift up and fly. After the experiment, the individuals were killed and the remaining wing was measured.

2.5. Selection intensity on male size

The selection intensity (Falconer 1981) on male size was calculated as shown in Arnold and Wade (1984) for cross-sectional data. The selection differential was calculated as the change in mean size before selection (searching males) and after selection (paired males). The intensity of selection is the selection differential divided by the standard deviation of size before selection. The significance of selection intensity was determined by comparing the mean size of paired males with the mean size of searching males with ANOVA.

3. Results

3.1. Temporal occurrence of searching males and ovipositing pairs

The average number of males in the vicinity of 1-hour-old droppings was 34.3 ± 12.9 (mean ± *S.D.*), whereas there were only one or two males on the dropping (Fig. 1). Thus, most mate-searching males in *S. inquinata* stayed on the surrounding vegetation during the 5.5-h observation period. The number of single *S. stercoraria* males on the same droppings always exceeded that of single males or pairs of *S. inquinata* (Fig. 1).

3.2. Male searching behaviour

Most males perched on the vegetation around droppings making frequent short flights (19.2 ± 4.4 changes per min, mean ± *S.D.*, $n = 9$). They were often attacked by conspecific males (2.2 ± 2.4 times per min) and also frequently attacked conspecific males (1.3 ± 0.9 times per min). There were no males of the yellow dung fly around droppings.

If males visited the dropping, the visit was very short. The average visit time was 32 ± 20 s (mean ± *S.D.*, $n = 19$). During their visit, they were continuously attacked by the yellow dung fly (0.7 ± 1.0 times per 10 s). Males of *S. inquinata* attacked mostly conspecific pairs (86 % of attacks) but also males of the yellow dung fly (altogether 0.9 ± 0.8 times per 10 s).

3.3. Pair formation

Of the 32 pairs observed starting copulation or oviposition on the dropping, only two were formed at the dropping. The others flew close to the dropping and then walked to it.

During oviposition, the female was guarded by the male. Pairs on the dropping were attacked 3.7 ± 2.1 times per min ($n = 14$). Most of the attackers belonged to the yellow dung fly. The frequent attacks sometimes resulted in the pair leaving the dropping (3 out of 14 pairs). These kinds of attacks resembled take-overs common in the yellow dung fly, and on one occasion a yellow dung fly male attempted to copulate with a *S. inquinata* female. Seven conspecific take-over attempts were observed, none resulting in a take-over. Once an *S. inquinata* male unsuccessfully attempted to mate with a yellow dung fly female.

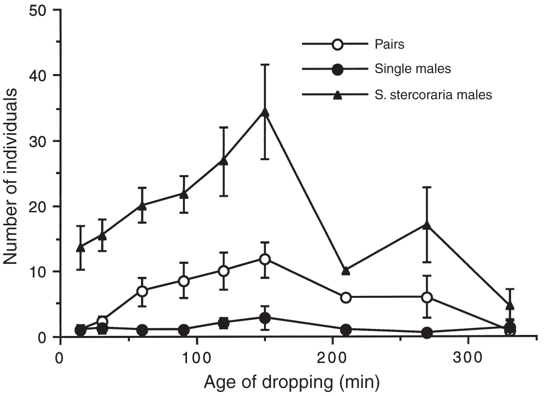

Fig. 1. Temporal distribution of searching males and pairs in *S. inquinata* and searching males in *S. stercoraria* on cow droppings. Mean and *S.D.* are shown.

3.4. The size of males and females

None of the three size distributions differed significantly from the normal distribution (Kolmogorov-Smirnov test for goodness of fit: searching males: $Z = 0.643$, $n = 225$, $P = 0.803$; mating males: $Z = 0.474$, $n = 128$, $P = 0.978$; females: $Z = 1.076$, $n = 128$, $P = 0.197$; Fig. 2).

Females, paired males and searching males differed significantly from each other in size (ANOVA: $F = 12.719$, *d.f.* = 3.511, $P < 0.001$). A post hoc test showed that males searching on the dropping (5.8 ± 0.7; mean ± *S.D.*) did not differ significantly from searching males around the dropping (6.0 ± 0.7)(Tukey-test: MD – 0.233, n.s.). Mating males (6.3 ± 0.7) were significantly larger than searching males on the dropping (MD = – 0.564, $P < 0.001$) or around it (MD = – 0.330, $P < 0.001$). Also females (6.3 ± 0.7) were larger than searching males on the dropping (MD = 0.539, $P < 0.001$) or around it (MD = 0.306, $P < 0.001$). The difference in size between females and paired males was not significant (MD = – 0.025, n.s.). In pairs, male size was positively and significantly related with female size (Fig. 3). Selection intensity for male size was 0.49.

3.5. A test on flying ability while in copula

I tested 27 pairs for flying ability. None of the 12 pairs with manipulated female wings were able to fly. In contrast, all 15 pairs with manipulated

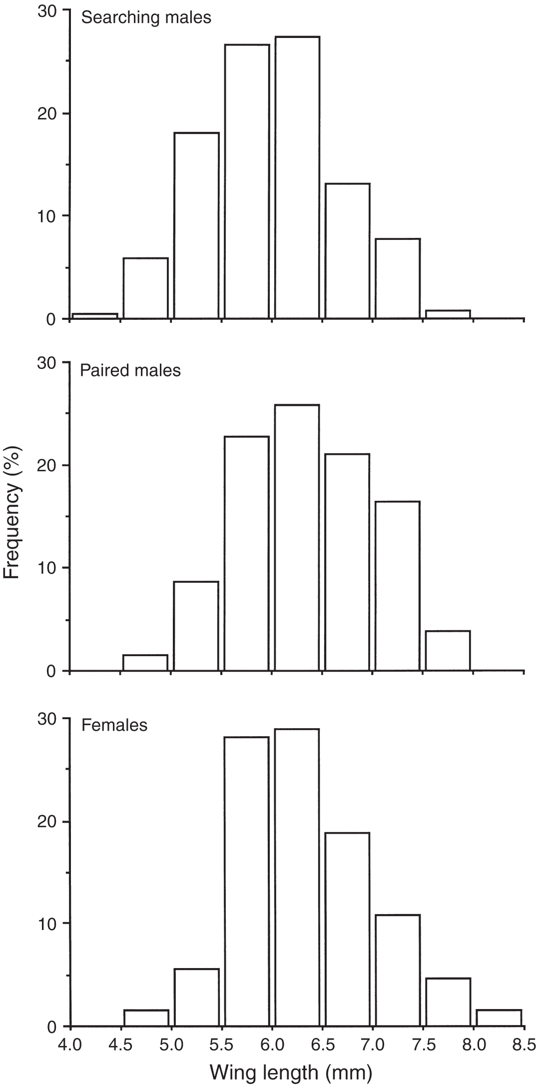

Fig. 2. Size (wing length) distribution of searching and paired males, and paired females in *S. inquinata*.

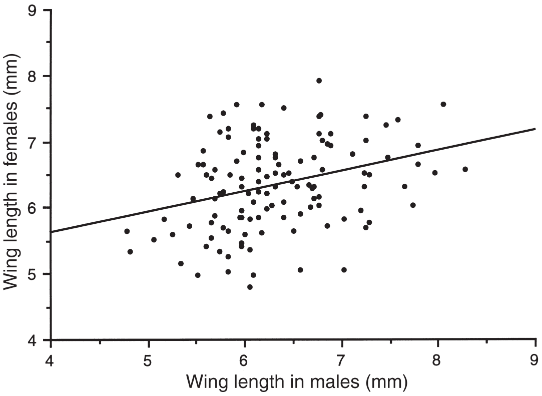

Fig. 3. Male size against female size in copulating pairs. The regression line is: $y = 4.455 + 0.299x$; $r^2 = 0.095$, $t = 3.629$, *d.f.* = 1, 126; $p < 0.001$.

male wings flew either directly to the window (12) or were able to lift off from the floor (3). Although males held the female wings during copula, females released their wings before take-off.

4. Discussion

In *S. inquinata*, males arrived at female oviposition sites in large numbers, and were frequently involved in aggressive encounters with conspecific males as well as with males of the yellow dung fly. Aggressive interactions between males are likely to favour large male size and, as expected, in *S. inquinata*, copulating males were larger than searching males. The selection intensity, which measures the force of sexual selection on male size, was 0.49, suggesting a strong selection on larger male size. For comparison, in the yellow dung fly, selection intensity on male size varied between 0.95 and 0.46 during the flight season (Otronen 1996). However, in the yellow dung fly, males are the larger sex (Otronen 1993), whereas — despite the apparent selection for large male size — in S. *inquinata*, females were the larger sex.

One major difference in the mating behaviour between *S. stercoraria* and *S. inquinata* is the sex able to fly during copula. In *S. inquinata*, females fly and carry the copulating male. This may be one factor contributing to the opposite sexual size dimorphism in these two closely related species. For example, in many butterflies, females carry males during flight and it has been suggested that this favours female-biased size dimorphism (Singer 1982). The origin of female-biased size dimorphism can be related with the advantage that large females enjoy by being able to produce large egg batches (see e.g. Wiklund & Karlsson 1988). In species where females carry males, loading constraints could contribute to the maintenance of female-biased size dimorphism. When comparing sexual dimorphism in waterstriders, Fairbairn (1990) found that although loading constraints did not explain female-biased sexual dimorphism, loading constraints which increased with increasing copulation time, explained a significant proportion of the variation in size ratio among mating pairs.

Pairs in *S. inquinata* were size-assortatively mated. Assortative mating can have many different causes (Crespi 1989), and my data only allows for the discussion of some of the possible ones. First, if small males are not able to defend their mate, assortative mating could partly result from male–male attacks against pairs. This has been show to cause assortative mating in the yellow dung fly (Otronen 1993). Although the conspecific attacks did not result in take-overs, the interspecific ones did, and could contribute to the assortative mating pattern. Second, flight in copula could also discriminate against disassortatively mated pairs. In a dance fly, where males fly with females, pairs with too heavy females were not able to fly and separated, and thus, male load-lifting capacity resulted in assortative mating (Marden 1989). In *S. inquinata*, female load-lifting capacity could cause assortative mating, pairs with too large males not being able to fly. In the yellow dung fly, pairs arriving from other droppings had relatively smaller females and stronger assortative mating compared with pairs formed at the dropping (Otronen 1993).

The copulation and oviposition in *S. inquinata* was strongly disturbed by the males of the yellow dung fly. In the yellow dung fly, the average wing length of searching males collected from the same farm as the *S. inquinata* males was 7.7 mm (Otronen 1996), whereas males of *S. inquinata* were almost 2 mm smaller, the average wing length being 6.0 mm. Therefore, it is likely that attacks by *S. stercoraria* males are more severe than those by conspecific males. This frequent disturbance by a larger species could be one reason why *S. inquinata* is found only in woods, and not on open pastures where *S. stercoraria* is very abundant. This interspecific interference could also explain why *S. inquinata* males spend hardly any time on the dropping during mate searching. Thornhill (1987), when examining interspecific fights for food among scorpionflies, found that the mating behaviour of the less-successful species was much more affected than that of the superior competitor. In *S. inquinata*, the significance of interspecific interactions affecting the mating system could be further examined in mating sites where the yellow dung fly can be excluded.

In conclusion, in spite of the male–male competition at the dropping, and sexual selection on large male size, females were the larger sex in *S. inquinata*. Although size trends in males and females can be caused and maintained by several factors (Hedrick & Temeles 1989, Fairbairn 1990) not examined in this study, the loading constraints during flight in copula may be one factor that contributes to the maintenance of female-biased size dimorphims in *S. inquinata*.

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