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Male mating preference for female survivorship in the seaweed fly *Gluma musgravei* (Diptera: Coelopidae)

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The seaweed fly mating system is characterized by pre-mating struggles during which females exhibit a mate rejection response involving kicking, shaking and abdominal curling. Males must resist rejection until females become passive and allow copulation to take place. However, despite the vigorous nature of the struggle males frequently dismount passive females without attempting copulation. Here we show that rejected females suffered higher post-encounter mortality rates than those accepted by males in the seaweed fly *Gluma musgravei*. Furthermore, we show that males also preferentially mounted females with higher future longevity. We propose that this male mate choice for female survivorship has evolved as a result of females often having to survive for long periods after mating until suitable oviposition sites become available. Such male preferences for female survivorship may be common in species in which oviposition must sometimes be substantially delayed after mating.

Keywords: sexual selection; longevity; male choice; mate rejection; pre-mating struggle

1. INTRODUCTION

In many animal species, the overall reproductive success of a male is predominantly determined by the number of females he inseminates during his lifetime. However, male mating capacity is not infinite and can be limited by the cost of producing ejaculates (Dewsbury 1982). When the availability of females exceeds male mating capacity, they will benefit from mating with those females with the highest potential fecundity (Berven 1981). Indeed, males have been found to prefer to mate with large females in species in which egg load and body size are correlated (Berven 1981; Shuster 1981; Loiselle 1982; Verrell 1982; Sargent *et al*. 1986). In some species females have exploited such a preference, for example males of the long-tailed dance fly *Rhamphomyia longicauda* must provide females with a nuptial gift and select females with the most inflated abdomens. However, non-gravid females can deceive males about their current egg load by artificially inflating their abdomens in order to receive additional nuptial gifts (Funk & Tallamy 2000).

Males in two groups of sciomyzoid flies, the dryomyzids (Otronen 1984) and the coelopids (Pitafi *et al*. 1990), appear to be able to exercise preferences directly on the basis of female egg load. The coelopid mating system is based upon sexual conflict (Day & Gilburn 1997; Crean & Gilburn 1998; Crean *et al*. 2000) and bears considerable similarity to the pond skater (Gerridae) mating system (Rowe *et al*. 1994). Males attempt to harass females into mating with them. Females are generally reluctant to mate resulting in a pre-mating struggle during which females perform a range of behaviours aimed at dislodging mounted males and, thus, preventing copulation. Large males gain a mating advantage in all coelopids so far studied (Crean *et al*. 2000). This occurs as a result of the higher resisting ability of large males (Crean & Gilburn 1998) and in some species appears to be increased by female preferences for large males, probably in order to avoid the greater costs of attempting to reject them (D. W. Dunn, C. S. Crean and A. S. Gilburn, unpublished results).

Even though pre-mating struggles can be extremely vigorous, male coelopids often exercise mate choice and dismount passive females without attempting to copulate with them. *Coelopa frigida* males commonly reject females that have recently oviposited (Pitafi *et al*. 1990). However, males also sometimes reject fully gravid females. Thus, an additional explanation for male rejection behaviour is required. Male coelopids do not appear to discriminate between females on the basis of size (Dunn *et al*. 1999), even though size is associated with female fecundity (Butlin & Day 1985). One possible explanation for the rejection of gravid females is that they are avoiding copulations with those females who are unlikely to survive long enough for suitable oviposition sites to become available. Female coelopids oviposit on deposits of seaweed, known as wrack beds, which are washed up above the high tide mark on beaches. Prolonged and unpredictable absences of wrack beds occur at many if not most sites on which coelopid populations are found (Butlin *et al*. 1984; Day & Gilburn 1997). Therefore, males may benefit from mating with females with good survival prospects, as they are more likely to be alive when the next wrack bed is deposited. Mate choice on the basis of future survivorship has not been previously reported in any species. However, male mate choice on the basis of female age, which may act as an indicator of potential survivorship, has been found

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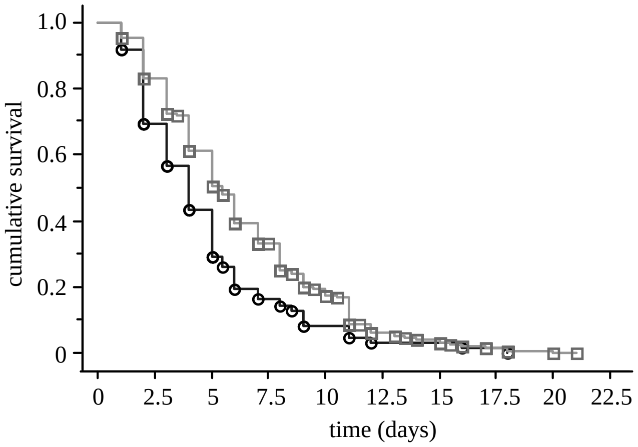

Figure 1. Cumulative survival frequencies of females that were mounted (squares) or not mounted by a male (circles).

(Rutowski 1982). Here we investigate male mate choice on the basis of female longevity in the Australian seaweed fly *Gluma musgravei*.

2. MATERIAL AND METHODS

The flies used were from a laboratory strain established from a collection made in 1997 from Mallacoota Bay in Victoria, Australia. We collected virgin adults shortly after eclosion and stored them at 4 °C with 5% sucrose solution as a food source. Under these conditions flies age very slowly and can live for several months. Flies were used immediately after collection if possible and were never stored for more than one week before use in the experiment. We transferred females to 25 °C for a two-day period with 5% sugar solution as a source of food and water. We also stored males for a two-day period at 25 °C. However, they were maintained in individual pots containing minced seaweed (mixed species of *Fucus* collected from Llandudno, Wales). We placed males and females together in pairs and noted whether or not the male attempted to mount the female within a 5 min period. When a male did attempt to mount a female the outcome of the pre-mating struggle was scored as an acceptance if the pair copulated, a female rejection if the female successfully dislodged the male during the pre-mating struggle or a male rejection if the male actively dismounted a female whilst she was passive. The duration of time a pair remained coupled was determined for those pairs that did copulate. *Gluma musgravei* couple for *ca.* 90 s with two or more copulations usually occurring during this period. Once a trial had been completed the females were individually placed in vials at 26 °C with 5% sucrose solution as a source of food and water. The life span of all females was determined by checking survival on a daily basis. The size of each adult was estimated from its wing length.

Any association between male mating behaviour and either future female survival or body size was determined using likelihood ratio χ^2-tests from logistic regression analysis. Female longevity was log transformed prior to use in the logistic regression analysis. Multiple logistic regression was used in order to remove variation in male willingness to mount associated with female size before retesting for an association between male willingness to mount and female survival. Linear regression was performed in order to determine whether the duration of coupling was associated with adult size or female longevity. Both coupling duration and female longevity were log transformed prior to performing the analyses

Table 1. *The association between male mating behaviour and both female future survival and body size in* G. musgravei

(Significance levels were determined using likelihood ratio χ^2-tests from logistic regression analysis. Standard errors are given in parentheses. Female longevity was log transformed prior to performing the regression analysis.)

	character		
	female size (mm)	female longevity (days)	male size (mm)
male mounted	5.28 (0.02)	6.27 (0.17)	5.45 (0.03)
male did not mount	5.09 (0.06)	4.75 (0.44)	5.76 (0.09)
χ^2-statistic	9.56	10.35	13.36
p-value	0.002	0.001	< 0.001
male accepted	5.29 (0.02)	6.45 (0.18)	5.41 (0.03)
male rejected	5.23 (0.06)	4.68 (0.38)	5.80 (0.05)
χ^2-statistic	1.00	7.50	18.65
p-value	0.32	0.006	< 0.001
female accepted	5.33 (0.03)	6.91 (0.25)	5.45 (0.03)
female rejected	5.23 (0.04)	5.77 (0.26)	5.33 (0.05)
χ^2-statistic	2.83	10.94	15.71
p-value	0.093	< 0.001	< 0.001

3. RESULTS

We determined whether male mounting was associated with female size or future survival in *G. musgravei* (table 1). Males were found to mount large females and females with higher future longevity preferentially (figure 1). Female longevity was strongly associated with female size ($F_{1,576} = 99.7$ and $p < 0.001$). However, when variation in male willingness to mount associated with female size was removed in a logistic regression model, the residual variation in male willingness to mount was still found to be associated with female survival ($\chi^2 = 4.87$ and $p = 0.027$). Thus, males seemed to prefer to mount long-lived females irrespective of the association between female survival and size.

Females that were dismounted by a male suffered a higher mortality rate than females that were not dismounted (figure 2). Unlike male mounting, male dismounting was not associated with female size (table 1). However, male dismounting was associated with male size, with larger males being more likely to reject a female.

Females that copulated were slightly larger and longer lived than females that rejected their males (table 1). Males that were accepted by a female were larger than successfully rejected males. This is consistent with an earlier study of *G. musgravei* that also demonstrated a considerable mating advantage of larger males (Crean *et al.* 2000). Coupling duration was negatively associated with male size ($F = 12.07$ and $p < 0.001$) and positively associated with female size ($F = 9.16$ and $p = 0.003$), but

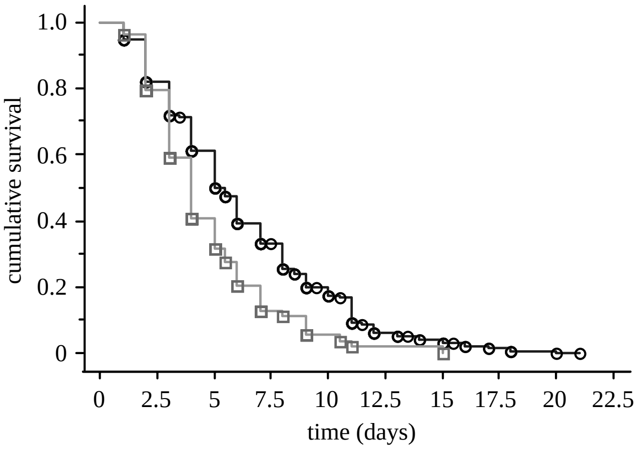

Figure 2. Cumulative survival frequencies of females that were accepted (circles) or dismounted by a male (squares).

was not associated with future female longevity ($F = 2.05$ and $p = 0.154$).

4. DISCUSSION

Male *G. musgravei* were found to mount potentially long-lived females preferentially. Furthermore, they were also found to be able to assess potential female survivorship whilst mounted, thereby enabling them to avoid mating with females with poor survival prospects. Thus, males may avoid wasting time, sperm and other components of ejaculates, such as accessory products, by not mating with those females that are least likely to survive long enough to lay their eggs successfully. Males also avoided mounting small females, who were likely to have lower egg loads, thus also avoiding wasting energy in pre-mating struggles with females of lower potential fecundity. They also coupled for longer when accepted by large females. However, males did not preferentially dismount small females prior to mating, presumably as more important indicators of potential fecundity, such as gravidity and potential survival, are assessed once a male is mounted.

There may be considerable opportunity for male mate choice in coelopids as population densities are often very high, providing males with almost unlimited opportunities for mounting females. Thus, supplies of sperm and other ejaculate components might well become limited, predicting that males should invest most in females with the highest potential fecundity. It is therefore surprising that male mate choice for large females is rare in coelopids (Dunn *et al.* 1999) as female size is associated with fecundity. It remains unclear why species other than *G. musgravei* do not exhibit such choice. One possible explanation is that supplies of sperm or other components of the seminal fluid may be less likely to become exhausted in those species not exhibiting male mate choice for large females, for example as a result of lower population densities or more reluctant females. However, there is currently no evidence in favour of either hypothesis. We are currently investigating whether other species exhibit mate choice on the basis of future female longevity. If supplies of sperm and other seminal components do not become depleted in these species then no form of male mate choice, either for large or long-lived females, would be predicted.

It is not clear what reliable indicator males use in order to assess potential female longevity. Much but not all of the association between male willingness to mount and female longevity occurred as a result of males preferring large females. However, when mounted, males can distinguish between potentially long-lived and short-lived females irrespective of their size. As the females used were of similar age, male *G. musgravei* can also exhibit mate choice on the basis of female longevity in the absence of choice on the basis of age. It is possible that males gain information about a female's survival potential from their struggling ability. Male coelopids also commonly rub their forelegs across the female's antennae. This might provide information about female fitness.

Large males were found to be less likely to mount. This is a common finding in coelopids (Dunn *et al.* 1999). They were also more likely to dismount and to couple for shorter periods than small males. These three observations suggest that large males are more selective in their choice of mate than small males. They will have more opportunity for exhibiting mate choice as they are better able to overcome female resistance during pre-mating struggles and, thus, have more opportunities for inseminating females. In contrast, when a small male does manage to overcome female resistance it should probably mate with that female, unless the female's potential fecundity is extremely low, as it may not manage to overcome the rejection response of another female for some time.

Male size has previously been found to be negatively associated with copula duration in the yellow dung fly *Scatophaga stercoraria* (Parker & Simmons 1994) and the pond skater *Gerris lacustris* (Daniellson 2001). Two factors have been proposed for favouring a shorter copula duration for large male dung flies: the faster rate at which they displace the sperm of other males and their shorter search times as a result of performing 'takeovers', during which large males displace mounted smaller males (Parker & Simmons 1994). Male coelopids frequently attempt such takeovers with the larger male invariably winning the resulting contest. Females coelopids also frequently remate and, thus, both of these factors could also play an important role in the evolution of the shorter copula durations of large male coelopids. *Gerris lacustris* has a mating system very similar to that of *G. musgravei*—large males gain a mating advantage in pre-mating struggles. In *G. lacustris* small males not only mated for longer but also achieved higher fertilization success from each mating. The similarity between the gerrid and coelopid mating systems might also extend to small male coelopids exhibiting higher fertilization success.

Mating has been found to be associated with reduced female survivorship in several species of Diptera (Chapman *et al.* 1995, 1998). This reduction in survival appears to occur as a side-effect of the accessory gland products passed by the male with their sperm. These substances stimulate oviposition and inhibit females from remating. Here we showed that mated female *G. musgravei* actually live longer than unmated females. This may well occur as a side-effect of a positive association between female size and female acceptance. This seems surprising as large females would be expected to be better equipped for rejecting males and, thus, be less likely to accept them. The explanation for this may lie in the fact that large males are more likely to have exhibited mate choice in favour of large females at the mounting stage, thus generating size assortative mounting. Large males are likely to be harder to reject, in which case larger females will have had a much harder task in rejecting their given male. Indeed, when variation in male size was controlled for, no association was seen between female acceptance and female size.

Mating has been found to increase female longevity in some insects (Oberhauser 1997). However, this effect appears to be restricted to species in which the males produce nutrient-rich spermatophores. Coelopids do not produce spermatophores and mate for only *ca.* 90 s. Thus, it is unlikely that any nutrients are passed to the female. The vigorous and ubiquitous nature of female rejection responses in coelopids also argues against a longevity benefit from mating.

The absence of a reduction in longevity in mated females is not surprising as it will not be advantageous for a male to increase female post-mating mortality if there is a considerable delay between mating and oviposition. Furthermore, the stimulation of oviposition will also carry a similar cost as the male's sperm would be wasted if females are stimulated to oviposit in the absence of suitable media. Thus, male coelopids should avoid the use of accessory gland products associated with either oviposition stimulation or a reduction in longevity. This applies to males in any species in which oviposition may need to be delayed after mating.

Here we showed that female *G. musgravei* that were rejected by males suffered higher mortality rates than accepted females. Thus, it appears that male rejection has evolved in order to avoid mating with females with a low life expectancy and small egg loads. Male mate choice for female survivorship has probably evolved as a result of females often having to survive long periods after mating until suitable oviposition sites become available. Mate choice for female survival is a novel finding. However, similar mate preferences for good female survivorship are predicted in any species in which there can be an unpredictable time-delay between mating and oviposition.

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