

MATE SELECTION IN THE FLY *SCATOPHAGA STERCORARIA*: FEMALE CHOICE IN A MALE-CONTROLLED SYSTEM

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Abstract. Sexual pairing in the fly *Scatophaga stercoraria* involves 'capture' of females by males. Size-related choice by males and females is considered, because these flies are highly variable in size, and size strongly affects reproductive success. Results show that males do not discriminate among females on the basis of size. Females choose large males when free to select mates. They move toward larger males when confronted by more than one possible mate, and their movement on the oviposition site takes them to areas where large males are more common. Females paired with large males gain from (1) reduced harm in struggles; (2) more rapid copulation and oviposition, with lower risk to the female and her progeny; and (3) greater ability to escape danger during copulation. These benefits may account for female preference for large males.

Typical male-female interactions in the fly *Scatophaga stercoraria* (Diptera: Scatophagidae) involve 'capture' of sexually receptive females by males. The extensive courtship displays of the sort found in most animals, including many insects, are absent (Parker 1970d). During the mating season both sexes of *Scatophaga* are common around fresh cow droppings or pats. Females use the pats as oviposition sites, and males move to these sites to capture mates. Males copulate with females immediately after capture and then guard the females, preventing further copulations, as they oviposit (Hammer 1941; Foster 1967; Parker 1970a, 1970b, 1970d, 1970e, 1970f; Borgia 1979). At low male density (< 10 males/pat) males actively exclude other, usually smaller, males from pats; while at higher male density per pat (> 10 males/pat), males scramble to capture females (Borgia 1980).

Even with limited courtship, individuals of each sex may exhibit significant biases in mate preference in their attempts to maximize reproductive gain. Although males may control females as mates and, to a large extent, limit female choice among males, it is unlikely that a male can extinguish all influence a female may have over the choice of a mate. Only a few detailed field studies of intraspecific competition in mate selection have been conducted, and these have been restricted to species in which females largely control the mate selection process (e.g. Lill 1976; Howard 1978; Thornhill 1976; Bradbury & Vehrencamp 1977). In this paper evidence for non-random patterns of mate selection by both sexes in the mate-capture

breeding system of *Scatophaga* are examined. Size is highly variable within each sex; this study examines male size both as a factor influencing male mating strategies and as a criterion for female choice among males. I also consider choice patterns of each sex in relation to male density on pats.

Methods

Observations were made of male and female behaviour on dung pats in a pasture 5 km southwest of Ann Arbor, Michigan. Observations totalling 92 h of female movement on pats and concurrent male behaviour were made in late June and early July of 1977. During this period flies were active on pats only 2 to 3 h daily, and there were commonly fewer than 10 males per pat. Such low-density conditions were chosen because relatively few males were on pats, and females could easily be observed before they were captured by males. Observations of female movement were made on pats that I shaped in the form of a cone with a pinnacle approximately 12 cm high and a base 18 cm in diameter.

Additional observations of male and female behaviour were made, unless otherwise stated, when flies were abundant either earlier in the spring of 1977, or in the fall of that year. Flies were measured photographically or by calipers after capture. Individuals under observation were marked with enamel paint (see Borgia 1980). Duration of events was measured using stopwatches.

Wild-caught females were used for fecundity measurements. Females were captured while they were copulating or as they arrived at a fresh dung pat after copulating, and were then allowed

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to oviposit in the laboratory on small dabs of dung; eggs were then counted.

Experiments to test flight ability of paired flies of different size were performed at 16 C using wild-caught pairs. I tested the flies by rapidly moving my hand 10 cm behind the pair. Pairs were scored as able to fly if they moved more than 10 cm.

Delay in completion of oviposition due to takeover attempts by males was computed from field observations of amplexing pairs involving males of different size. Pairs were observed from the initiation of copulation to the completion of oviposition. The male and female of each pair were marked to facilitate recognition. Delay in oviposition was calculated as the sum of time spent off the pat by the female from the time copulation was initiated to the time oviposition was completed.

Statistical analyses include simple linear regression (Draper & Smith 1966), Spearman's ρ (Conover 1971), and t -test (Wonnacott & Wonnacott 1972). Means are designated by $\bar{X} \pm 95\%$ confidence intervals.

Male Choice of Females

Males are commonly viewed as the sex that specializes in quantity of mates even at the expense of some mate quality (Bateman 1948; Trivers 1972). This characterization is based on the assumption that a male provides relatively inexpensive gametes to females, presumably leaving a male with sufficient reserves to inseminate many females. By contrast, the expensive pre-fertilization investment in ova by females leaves them with little potential for gain from multiple matings.

Male contributions at the time of mating appear to be small relative to female investment in gametes. Because males seem not to be limited by a shortage of sperm (see below), it might be predicted that males would not discriminate among females. However, males do allocate time to copulation and guarding during oviposition, and this time investment might cause males to discriminate among females. Male gain from rejection of some females may be analysed in terms of optimal time expenditure in fertilizing eggs (Parker 1974). Large females tend to lay more eggs than small females (Fig. 1; see Parker 1970c, Fig. 1). Consider the male that captures a small female soon after a pat is dropped. This is the time when most females have not yet arrived at the pat, and numerous other males are there seeking females. Such a male has the option

of copulating and guarding the female or, if she is small, rejecting her and searching for a larger female. A third option, copulation with a female and then immediately releasing her, has been shown to be unprofitable due in part to the pattern of sperm precedence, which favours the last male to copulate before oviposition (Parker 1970c).

Male gains from preference for large females should be most important under conditions of high male density because most females arrive at fresh pats soon after deposition during a short period of time (Parker 1970a, 1970b). Males capturing females during this period begin a copulation and guarding of females that lasts approximately 45 min and ends after the number of incoming females has peaked (Parker 1970d; Borgia 1978). Thus males that amplex with a small female will miss the period when they are most likely to capture a larger female.

Results

Males commonly fight for females and are rarely seen to release them without copulating and then guarding the female until she completes oviposition. Of 212 wild-caught gravid females that I released on pats, 203 first encounters with males resulted in an attempt by the male to copulate with the female after he touched her. In no cases did a male reject a gravid female after he had attempted to insert his genitalia. The

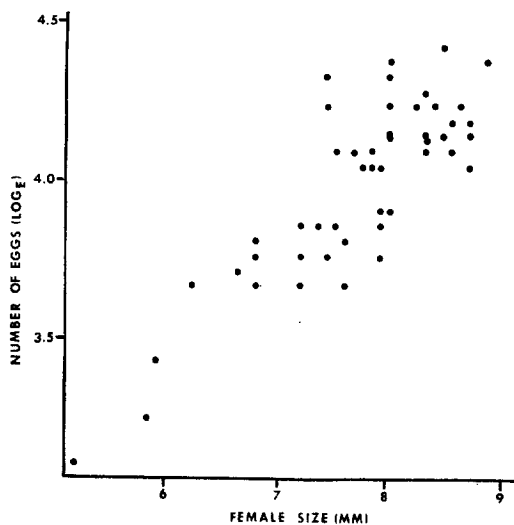


Fig. 1. Number of eggs laid by female versus female wing length. Regression equation is $Y = 0.31X + 1.58$, $R^2 = 0.726$, $P < 0.001$, $SE = 0.157$.

nine instances of male failure after touching them might be and perhaps discriminating mates, but it is more likely failed to recognize these rejections were directed towards would be expected that be smaller than females to encounter them. However, the difference between the (the mean of the rejected larger; $0.2 < P < 0.3$). nine females whose first in a copulation attempt the next male to meet the nine cases the second male first.

Additional evidence thesis that males commonly comes from the complete in which gravid females pats populated by males. 2000 h of observation of pats have I seen a gravid about on a pat occupying males without being attacked. Moreover, on fresh were densely populated males were extremely seeking attacks were other males. Thus female males or intersex flies observation), both of which the mate-seeking male.

Male errors in search are particularly common when related by males. At high reason for large males except in erroneous attacks. Among males actively small males are attacked their larger counterparts. Results suggest no tendency avoid attacks on small hypothesis that males among females.

In the fall of 1977 I observed were rejected after males their genitalia. All of the completed oviposition and checked for eggs. Ten or no ova (2.4 ± 1.67 , out).

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nine instances of male failure to mount females after touching them might be viewed as rejection and perhaps discrimination among possible mates, but it is more likely that the attacking fly failed to recognize these flies as females. If rejections were directed toward small females it would be expected that rejected females would be smaller than females captured by the first male to encounter them. However, I found no statistical difference between the two groups of females (the mean of the rejected group was numerically larger; $0.2 < P < 0.3$). Moreover, among the nine females whose first encounter did not result in a copulation attempt, all were amplexed by the next male to meet them, and in four of the nine cases the second male was larger than the first.

Additional evidence for rejecting the hypothesis that males commonly avoid small females comes from the complete absence of situations in which gravid females move unmolested on pats populated by males. In no case in more than 2000 h of observation of *Scatophaga* activity on pats have I seen a gravid female of any size move about on a pat occupied by more than three males without being attacked and sexually engaged. Moreover, on fresh pats and on those that were densely populated (> 10 males/pat), males were extremely active and most mate-seeking attacks were erroneously directed at other males. Thus females may be mistaken for males or intersex flies (Parker 1969; personal observation), both of which are of little value to the mate-seeking male.

Male errors in searching for mates are particularly common when pats are heavily populated by males. At high male density there is no reason for large males to attack other males, except in erroneous attempts to capture females. Among males actively searching for mates, small males are attacked more frequently than their larger counterparts (Borgia 1980). These results suggest no tendency for large males to avoid attacks on small flies, and support the hypothesis that males do not discriminate among females.

In the fall of 1977 I observed 17 females that were rejected after males had attempted to insert their genitalia. All of these females had recently completed oviposition and eight were captured and checked for eggs. These females carried few or no ova (2.4 ± 1.67 , $\bar{X} \pm 95\%$ CI throughout).

Discussion

Assuming that costs of activities in searching for mates are negligible, the relative success of a rejection versus a holding strategy can be determined by what Parker (1970c, 1970d) called 'egg gain' by males. A male that captures a female and completes the copulation-oviposition sequence has a gain rate determined by the female's size; her size, in turn, determines both her fecundity and the time it takes to complete the sequence.

Under most conditions, the great majority of females who oviposit in a pat arrive very soon after a pat is deposited. Males who remain with the first female they capture miss opportunities to copulate with other females. Males using the option of rejecting females must find a larger female during this period to make a rejection strategy successful. Males who reject a small female expect PN eggs, N being the mean number of eggs carried by females arriving at the pat and P the probability that a male will capture another female on that pat. So for rejection to be a better strategy

$$PN > m$$

where m is the number of eggs carried by the largest female males reject. The probability of a male finding another female can be estimated using the sex ratio of flies found around pats. Approximately two males per female is the lowest sex ratio found on pats with high (> 10) numbers of males per pat (sex ratios from 4:1 to 8:1 are much more common; Borgia, in preparation). The average size from a sample of 49 females is 7.4 mm and such a female, according to a regression of size and egg number, will carry approximately 48 eggs. Substituting into the above equation, where $P < 0.5$, for rejection to be profitable a rejected female must carry fewer than 50% of the number of eggs carried by the average female. Such a female would be 4.45 mm, much smaller than 4.9 mm, the size of the smallest female found in nature. Thus the absence of any tendency for males to reject females agrees with predictions we might make from rates of egg gain for males.

Recognizing that large males have greatest access to females might suggest that the model for rejecting females would underestimate the size of females which should be rejected by large males. However, there is a compensating factor that makes this model robust. On pats with high densities of males, males tend to be larger than the mean for the population (Borgia 1978). Thus

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 $Y = 0.31X + 1.58$,

males used in computing the sex ratio of males in the vicinity of the pat are relatively equal as competitors for females.

The fact that females of any size arriving at a pat already occupied by males have little difficulty finding a mate does not eliminate the possibility that some classes of males reject small females. Large males have been shown consistently to be overrepresented in samples of amplexing flies. They occupy positions where the capture of females is most likely (Borgia 1978, and below), and therefore might be expected to gain most from a strategy involving rejection of small females. Given the evidence above that unattached females are rare on pats patrolled by males, and the knowledge that if a female is to reproduce she must eventually come to a pat, I would predict a correlation of male and female size among mating pairs if small females are commonly avoided or rejected by large males. Sizes of amplexing pairs show no correlation (Fig. 2), suggesting that rejection does not occur even by large males.

It was suggested above that material investment by *Scatophaga* males appears to be small relative to that made by females. The smaller contribution of males can be shown by several lines of evidence. Males provide no material contribution to females other than sperm. There is no transfer of potentially valuable materials, and males do not exclude females or, in most

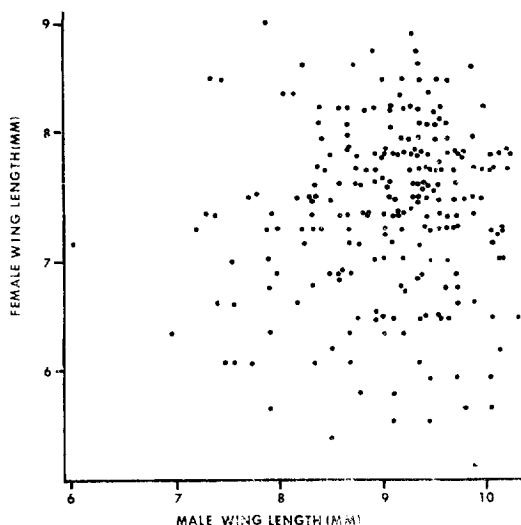


Fig. 2. Female wing length versus male wing length for paired flies. Regression statistics are $R^2 = 0.007$, $P = 0.207$, $SE = 0.777$.

cases, sexual competitors from the oviposition site. Parker's (1970c) work showed that males can provide four females with a full complement of sperm in one day, and that these males are able to replenish their sperm supply overnight. It takes females a minimum of four days after oviposition to develop a new set of yolked eggs. Moreover, after copulation, females, who lay all their mature eggs (up to 93) in a continuous oviposition, leave the pat immediately after eggs are deposited. By contrast, males typically remain on the pat and search for additional mates; one male copulated with and then guarded six different females in succession during one afternoon (Borgia 1978). Females arrive before mating with abdomens noticeably distended and leave with them obviously flattened after oviposition; males' narrower abdomens do not noticeably change in size. In laboratory tests, females died if not given food within 24 h after copulation (personal observation), but similarly tested males lived up to two weeks. These observations all support the argument that sperm transfer for males in mating is relatively inexpensive when compared to the costs to females of making ova.

Female Choice of Males

When investment in offspring by males is minimal, females are expected to be the more choosy sex. Choice of a male for genetic benefits or for aid he might give, albeit selfishly, during the copulation and oviposition process may become important. These benefits may influence a female's mating decisions because of her limited opportunity to gain from repeated matings and the ready availability of males as mates.

The capture of females may limit female ability to choose among males. However, females appear to have the opportunity to affect which males capture them. This choice by females may account for a portion of the success of large males noted above. Here I consider two types of evidence for size-related choice: (1) passive choice, i.e. movement of females to positions where they are likely to be captured by large males, and (2) active choice, i.e. movement toward or presentation to large males.

Passive Choice

Under conditions of low male numbers per pat, females exhibited a pattern of approaching and positioning on the pat that suggests a passive mode of selection for large males. With three to seven males on or within 25 cm of the pat,

there was commonly a male in the middle among males with the most males. Usually the largest, male patrolled the central and upward sides of the pat, while the smallest males on the periphery. The dominant male was almost always patrolling on and around the pat, and rejected males who did not come to them on the pat.

Thirty-one females were observed on patting pats. They landed 10 cm or more of the pat in the adjacent dung, and stayed lasting from 20 s to 4.2 min (mean $N = 8$), the females began moving toward the dung, pausing for a moment before males. Upon reaching the dung, they began moving up the surface toward the high point. Most females stayed on the pat until they reached the high point. Movements were jerky, and the body close to the dung. Most females of *Scatophaga* on the pat were the same as those of females of the *Scatophaga* phaga, which attempted to mate with *Scatophaga* males. Such a pattern makes it appear that females are avoiding males at least until they reach the top of the pat. Other females, however, crouched, jerky movements, and then moved themselves in a crevice or under the top of the pat, if they were not by a male they began to move.

Comparison of female positions on the pat with those who were captured midway showed that while the latter were not captured, the former moved onto the pat and laid eggs. I observed 10 females, and after allowing 10 min of dung found that 93.6% of their eggs had been laid by females moving to the top of the containers with fresh dung. Eggs from the top laid eggs; eggs from the bottom did not hatch. The numbers of 'virgin' and 'non-virgin' eggs were 10 and 10, and show a statistically significant difference ($\chi^2 = 9.0$, $df = 1$, $P < 0.01$) were captured by males and not them.

Among 23 females moving toward the male-density pats, 21 moved toward the pinnacle (17/18 on pats without males). None of the females came this close

from the oviposition showed that males with a full complement of these males are able to supply overnight. It was of four days after a set of yolked eggs. Females, who lay all (1993) in a continuous immediately after eggs, males typically refrain for additional mates; and then guarded six on during one after-arrival before noticeably distended and flattened after oviposition. Abdomens do not. In laboratory tests, food within 24 h after oviposition, but similarly in weeks. These observations support the argument that sperm storage is relatively inexpensive to females.

Choice of Males

Spring by males is expected to be the more likely for genetic benefits, albeit selfishly, during the mating process may be influenced by the limited repeated matings and males as mates. This may limit female choice. However, the opportunity to affect the mating process by this choice by a portion of the successful. Here I consider two related choices: (1) the choice of females to mate with large males, and (2) the choice of females to mate with large males.

When male numbers per pat are low, the pattern of approaching suggests a passive choice of large males. With three males in 25 cm of the pat,

there was commonly a dominance hierarchy among males with the most dominant, and usually largest, male patrolling and defending the central and upward sides of the pat and smaller males on the periphery (Borgia 1980). The dominant male was almost always the most active in patrolling on and around the pat, and he attacked males who did not move as he approached them on the pat.

Thirty-one females were observed approaching pats. They landed 10–15 cm from the edge of the pat in the adjacent grass. After a pause lasting from 20 s to 4.2 min ($\bar{X} = 2.7 \pm 1.93$, $N = 8$), the females began walking very haltingly toward the dung, pausing when approached by males. Upon reaching the pat edge the females began moving up the surface toward the nearest high point. Most females moved upward on the pat until they reached the top or pinnacle. Movements were jerky, with legs bent and the body close to the dung surface. Behaviour of female *Scatophaga* on the pat strongly resembled that of females of the larvoviviparous fly *Sarcophaga*, which attempted to avoid predation by *Scatophaga* males. Such similarity in movement makes it appear that female *Scatophaga* are avoiding males at least until they reach the top of the pat. Other females showed the same crouched, jerky movements; and after positioning themselves in a crevice approximately midway to the top of the pat, if they were not captured by a male they began to oviposit.

Comparison of females moving to the top of the pat with those who were beginning to oviposit midway showed the former to be virgins while the latter were non-virgins. All six females that moved onto the pat but did not continue to the top laid eggs. I captured three of these females, and after allowing them to oviposit in dabs of dung found that the great majority (93.6%) of their eggs hatched. Six of the 23 females moving to the top of pats were placed in containers with fresh dung. Only one of the six laid eggs; eggs from this one brood did not hatch. The numbers of females laying eggs in 'virgin' and 'non-virgin' groups were compared and show a statistically meaningful difference ($\chi^2 = 9.0$, $df = 1$, $P < 0.005$). Two females were captured by males before I could classify them.

Among 23 females moving to the top of low-male-density pats, 21 moved within 4 cm of the pinnacle (17/18 on pats with males, 4/5 on pats without males). None of the six ovipositing females came this close to the pinnacle before

capture by males ($\chi^2 = 19.85$, $df = 1$, $P < 0.001$). Time before capture by males of virgin and non-virgin females was also different. Virgins were captured much sooner (1.3 ± 0.9 min) than non-virgins (9.6 ± 6.9 min). Non-virgins placed large numbers of eggs into the pat before capture. Using Parker's (1970e) value of 2.2 eggs inserted per minute, these females oviposited approximately 26.2 eggs, or about one-half the number they carried, before being captured. Differences between groups in length of time between when they moved onto the pat and when they were captured shows the importance of female behaviour in influencing where and when they are captured by males. The significance of early oviposition without males is discussed below.

In a sample of 30 observed copulations at low male density per pat, dominant males captured most virgin (13/18), non-virgin (5/6), and unclassified (5/6) females. There was no statistically meaningful difference between the numbers of virgin and non-virgin females captured by dominants ($\chi^2 = 0.296$, $df = 1$, $P < 0.25$), who captured 77% (23/30) of the females arriving on pats that they controlled. The reciprocal of the number of unpaired males in the vicinity of the pat at the time a female was captured ($\bar{X} = 4.29 \pm 1.11$, $N = 12$) was used to determine the expected percentage of matings for each male present (23.3%). Comparison of expected and observed number of females captured showed that the dominant males gain a greater-than-expected share of copulations ($\chi^2 = 25.2$, $df = 1$, $P < 0.001$).

The situation is somewhat different when male density is high. Females tend to approach the pat from the upwind direction (Parker 1970b; Borgia 1978). Males who occupy this side of the pat are consistently larger than those on the downwind side (Borgia 1980); hence females are presented with males segregated by size and, by varying the direction of entry onto the pat, they have the opportunity to choose males on the basis of their size. The fact that females consistently approach from the upwind direction suggests that there is at least no disadvantage to mating with large males, and that perhaps females attempt to be paired with larger males.

Flies find fresh pats by flying upwind, following the odour of fresh dung. Parker (1970c) suggests that the reason for the upwind approach by females is that the females have flown past the source of the odour gradient and that they then move back to this source. Another ex-

planation is that females are better able to control capture by males with wind at their backs. Approaching from an upwind direction allows females to fly faster than males who must fly into the wind. The ability to control capture by males may be important to the female for several reasons, including the possibility to exercise male choice and to avoid potentially harmful situations in which several males simultaneously grasp her. That ability may also allow females to choose larger males.

Active Choice

Virgin females on pats occasionally displayed toward males (4/18 cases). Displays involve a rapid side-to-side rocking motion with occasional wing flicks and with the abdomen slightly raised. In every case, displays were effective in attracting the male toward which they were directed. Displays were sometimes used when females had the opportunity to choose between males. In one case a female was near the pinnacle, a small male moved toward her, and she flew off the pat into the grass in front of the larger/dominant male who had moved off the pat to search. She displayed, he quickly responded by grabbing her, and copulation ensued.

In the three other instances of displays, the females remained near the pinnacle. In two of these other instances, the female moved toward the larger of two males that had oriented toward her and appeared as though they would attempt to capture her. Such active avoidance of small males and movement toward large males suggest that females have a real preference for large males, and that observed biases are not simply a result of the female's greater ease in finding these males. In all instances on low-male-density pats where females had the opportunity for active choice between males who differed noticeably in size, the females moved toward the larger/dominant male (in 5 of 5 cases; $P = 0.03$, binomial probability). Females also chose larger males in 6 of 7 cases ($P = 0.11$) on pats with medium and high numbers of males where, apart from favouring the upwind portion of the pat, there is no preferred position. Thus there appears to be a statistically significant tendency for females to favour large males (11/12; $P = 0.003$).

Patterns of active choice by females, and high rates of success of large males under conditions where the females' behaviour appears to aid their capture by large males, indicate that females consistently favour mating with large males.

Active and passive choice may be important in determining patterns of male mating success. At low male density, where males of variable size are common around pats and females have an opportunity to choose, this choice may be especially important in determining size-related reproductive success among males.

Why Do Females Choose Large Males?

Recent models of mating systems have emphasized the importance of analysing the relative gain for females from particular patterns of mate choice (Trivers 1972; Borgia 1979). Below I consider several of the most likely reasons for female preference of large males.

Heritable Size Differences

In *Scatophaga* large males have greater success in controlling or gaining access to ovipositional sites, and have greater ability to replace males that are paired with females (Borgia 1979, 1980). Females might prefer large males as mates if these males offer heritable traits that are likely to enhance the fitness of their offspring. In particular, if large males tend to produce large sons, then the higher expected reproductive rate of these sons should form the basis for a pattern of biased mate selection among females. A study of the genetic heritability of size in *Scatophaga* showed no correlation between parent size and offspring size, and indicated that size variation among offspring could be explained by differences in larval growth conditions (Borgia 1979).

Male Protection of Females

Large males protect females from attack by other males, and this protection may be significant in several respects. Females paired to large males are less likely to be involved in damaging takeovers or related struggles (Borgia 1980). Hammer (1941) said that females may be drowned or torn to pieces. Parker (1970e) considered this claim 'exaggerated', but later (1978) appeared to agree that some significant damage to females may occur in these contests. Here I present evidence that struggles are costly to females, so that the observed pattern of pairing with large males may reduce the damage that females are likely to suffer in male attempts to capture them.

Results. The relatively low percentage of matings that were disrupted by attacks precluded systematic gathering of information on damage to females. Obvious instances of harm to females occurred when their abdomens were ripped apart

by contesting males and over the pat. Dismemberment occurred twice among females observed.

The best evidence for damage from male activities comes from which up to nine males of a female. Thirty-four from struggles that lasted involved three or more for their ability to fly. Six groups of contesting males fly or flew weakly even nine females taken from struggles flew either immediately a gentle prod after release ($P < 0.05$). These results of male protection from damage from attacks by

Other evidence that capture females may comes from the frequent damage among intersexes phologically similar to repeatedly attacked and they were females but and the wings of intersexes show much more severe damage females on the same pat that I captured and the

Discussion. Even though of females were noticeable intense male competition the extent to which females and pulled at by males suggests that undetected mon. Male fights to hold female or disengage and strain on the smaller female attackees sometimes for the wings from contact this behaviour can protect the female caught between involved in struggles with around a female have almost at any time, was focus of the fight and and loses interest. Thus it avoid damage by choosing more often allow them and return for later visit matured.

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The best evidence for frequent harm to females from male activities comes from struggles in which up to nine males fight for the possession of a female. Thirty-four females were removed from struggles that lasted at least 2 min and that involved three or more males, and were tested for their ability to fly. Sixteen females taken from groups of contesting males either were unable to fly or flew weakly even after I prodded them. All nine females taken from pairs not involved in struggles flew either immediately or when given a gentle prod after release ($\chi^2 = 4.23$, $df = 1$, $P < 0.05$). These results suggest that the quality of male protection may be critical in reducing damage from attacks by males.

Other evidence that repeated male attempts to capture females may cause the females harm comes from the frequency and extent of wing damage among intersex flies, which are morphologically similar to females. Intersex flies are repeatedly attacked and mounted by males as if they were females but are then released. Typically the wings of intersexes are severely shredded and show much more severe damage than males and females on the same pat. Nine of 14 intersexes that I captured and then released could not fly.

Discussion. Even though only a small fraction of females were noticeably damaged in struggles, intense male competition for females exists; and the extent to which females are twisted, stroked, and pulled at by males with stoutly bristled legs suggests that undetected damage may be common. Male fights to hold their own genitalia in a female or disengage another's must place great strain on the smaller females. Male attackers and attackees sometimes fold back wings to protect the wings from contact with other males, but this behaviour can provide little protection to the female caught between the two males. Males involved in struggles with several other males around a female have the option to disengage almost at any time, whereas females are the focus of the fight and are held until the last male loses interest. Thus it appears that females may avoid damage by choosing large males. This may more often allow them to complete oviposition and return for later visits after more ova have matured.

Rapid Oviposition

Coinciding with the protection from physical damage offered by large males is the more rapid completion of copulation and oviposition for females paired to these males. Parker (1970e) considered time loss to the female resulting from struggles and takeovers, but only in the context of delay in starting a new reproductive cycle. Perhaps more significant is the effect of such time delays on the survival of eggs, larvae, and the female herself. The oviposition site decays rapidly in quality, and even relatively short-term delays may have a significant impact on larval success. This decay reduces larval success and would favour early oviposition by females. Females that are able to oviposit into fresh pats allow their eggs time in the pat before parasites and predators arrive (see Foster 1967). Moreover, their eggs are likely to develop into larvae that (1) are larger, (2) have more moist dung available, and (3) are better able to endure sudden catastrophic events, e.g. opening of pats by birds, than those of females that oviposit later. Hammer (1941) states that the time from oviposition to hatching and successful migration of larvae into the pat may be the period of highest mortality in *Scatophaga's* life cycle. If this is so, moist dung may be a key factor influencing the survivorship of these first-instar larvae.

Perhaps the most important benefit to the female from rapid, uninterrupted copulation and oviposition is reduced probability of mortality. Risks of mortality and damage are high for a female near the pat, and these risks are proportional to the amount of time spent there. Females able to complete amplexus rapidly are likely to benefit in two ways. They will have a greater likelihood than other females of ovipositing all of the eggs they carry, as well as of surviving and returning to oviposit after they have matured more eggs.

Female abundance around pats was highest immediately after pat deposition, suggesting that oviposition in fresh pats is important (see Parker 1970b). Non-virgin females' attempts to oviposit without males supports the hypothesis that rapid oviposition improves reproductive success.

Results and Discussion. Struggles, takeovers, and recopulations after takeovers have been cited as primary causes of delayed oviposition. Intimidation by large males of small males paired with females on the pats is another reason for female preference of large males. Parker (1970f) showed that pairs may reduce the fre-

quency with which they are attacked by moving off the pat for copulation. These emigrations were most common on pats with large numbers of males. In my observations, 25 of 29 such movements on low-male-density pats were immediately preceded by an attack on the pair that moved. Emigration was also common for pairs that were attacked during oviposition. A male may fly off the pat with the female; in one case a pair with a previously ovipositing female remained off the pat for 149 min. Another male flew off the pat with his female four times during oviposition. Small males may also capture females and copulate for long periods ($\bar{X} = 96.4 \pm 14$ min) of up to 137 min. Often after long copulation the male released the female and did not guard her. Evidence for the importance of time delay due to takeover and its relationship to male size is shown for females paired to males of different size in Fig. 3. This Figure shows a negative rank correlation between the time delay experienced by a female in completing oviposition and the size of male with whom she was initially paired.

Often during these delays the female made what seemed to be attempts to move back to the pat or to force the male to bring her there. Females showed a 'bucking' movement that continued intermittently for several minutes. These

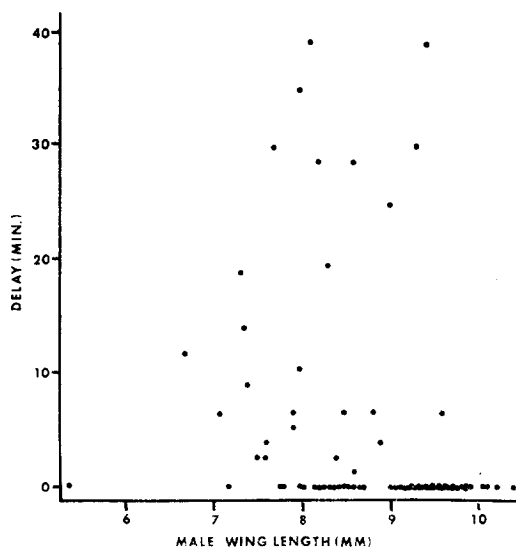


Fig. 3. Time delay due to takeovers versus male size. Results of rank correlation $\rho = -0.462$, $P < 0.01$.

movements appear to be significant, in that they commonly preceded either flying back to the pat by the male with the female, or the male's abandonment of the female. These movements were quite distinctive and, for the most part, occurred after the mean copula duration or when a male moving with a female on the pat stumbled after flying onto the pat. For example, bucking occurred in 17 of 19 cases in which the male held the female away from the pat at least 10 min beyond the normal copula duration. It appeared that these movements might attract attacks by other males and, in fact, might incite attacks, as Cox & Le Boeuf (1977) suggest occurs in the elephant seal (*Mirounga angustirostris*). However, I found no significant difference in attack rates due to female movements between non-moving pairs (0.069 attacks/min) and pairs that had 'bucked' within the last 5 min (0.098 attacks/min). Lack of a significant difference is not surprising given the low rate of attack and infrequency of female bucking for pairs off pats.

Small males often resist female attempts to move toward central positions of the pat. This behaviour may restrict female ability to utilize optimal ovipositional sites. In four cases small males, less than 8.5 mm in wing length, paired with females and repeatedly hooked their legs around those of the females as they moved up the pat surface, where there were large males and other ovipositing pairs. In seven additional cases where small males paired with females, these males appeared to resist strenuously female attempts to move toward the pat after the pair had exceeded the mean duration of copulations. As the female walked toward the pat the male grabbed grass stems and the females' legs, at times holding her only with his genitalia. One of these trips from the site of copulation to the pat extended for 32 cm and lasted 74 min. Presumably the cost of takeover for small males is so high that use of poor ovipositional sites is compensated by a reduced likelihood of takeover. Losses for females resulting from takeover may be less severe; hence the conflict between the males and females over the choice of oviposition sites. Other small males have been observed to have their mates oviposit in very small, apparently low-quality pats while other large pats were nearby (Borgia, in preparation). A small male that captures a female in a peripheral locality may be unable to bring the female to a good pat because of his limited ability to fly with her; hence the female may be forced to oviposit at the site where the male captured her, regard-

less of the number and oviposition sites.

Escape by Pairs

A male's ability to fly is important to both members of a pair. The ability of flies to move rapidly in their being crushed or amplexed to males are cannot be used to assist in flight of a pair depend upon the movement. Cows commonly s shortly before had many (Borgia 1978), and on se crushed flies. If the male fly only weakly with the to be crushed. The male n but males do this relucta late for the female to rea

Results. In order to male size in determining move his mate and h danger, I simulated a hand quickly near amplexed whether the male Afterwards I captured a male and the female. Fig of this experiment. The s to fly with females of a intermediate size have so large females. This relat significance at low tempe appear to have more diff in flight. Thus, at least a may be important for fe large males.

Discussion. The import females may be enhance ceptibility of *Scatophaga* paired. Davies (1977) re may be a primary item (*Motacilla alba*) in Eng measurements, he four average flies were most c assumed these flies were prey on pairs, which fly w unpaired males. Thus the might result from a large in samples used to estim field site I did not assess t birds. If predation appro suggests, then amplexus especially dangerous peri

In summary, female pr seems to be due to bene

ent, in that they back to the pat or the male's movements the most part, or when the pat stumbled simple, bucking the male held at least 10 min. It appeared act attacks by bite attacks, as occurs in the *rostris*). How- ence in attack between non- and pairs that 0.098 attacks/ ce is not sur- ck and infre- off pats.

attempts to the pat. This ability to utilize r cases small length, paired ed their legs ey moved up ge males and ditional cases males, these ly female at- the pair had ulations. As at the male ales' legs, at alia. One of on to the pat 4 min. Pre- all males is so sites is com- of takeover. takeover may between the oviposition observed to small, ap- r large pats). A small peripheral female to a to fly with to oviposit er, regard-

less of the number and size of males at good oviposition sites.

Escape by Pairs

A male's ability to fly with his mate is important to both members of a pair when the inability of flies to move rapidly is likely to result in their being crushed or eaten. Wings of females amplexed to males are held by the male and cannot be used to assist flight, so both members of a pair depend upon the male for rapid movement. Cows commonly step or lie on pats that shortly before had many *Scatophaga* on them (Borgia 1978), and on several occasions I found crushed flies. If the male is unable to fly, or can fly only weakly with the female, they are likely to be crushed. The male may fly off and leave her, but males do this reluctantly and may leave too late for the female to react to danger.

Results. In order to test the importance of male size in determining the male's ability to move his mate and himself from potential danger, I simulated a disturbance by moving my hand quickly near amplexing pairs. I then recorded whether the male flew with the female. Afterwards I captured and measured both the male and the female. Figure 4 shows the results of this experiment. The smallest males are unable to fly with females of any size, and males of intermediate size have some difficulty flying with large females. This relationship takes on special significance at low temperatures, at which males appear to have more difficulty carrying females in flight. Thus, at least at cool temperatures, it may be important for females to associate with large males.

Discussion. The importance of male flight with females may be enhanced by the increased susceptibility of *Scatophaga* to predation while paired. Davies (1977) reports that *Scatophaga* may be a primary item in the diet of wagtails (*Motacilla alba*) in England. Using wing size measurements, he found that smaller-than-average flies were most commonly eaten. Davies assumed these flies were males, but birds may prey on pairs, which fly with more difficulty than unpaired males. Thus the small size of prey items might result from a large proportion of females in samples used to estimate prey size. At my field site I did not assess the level of predation by birds. If predation approached the levels Davies suggests, then amplexus with males may be an especially dangerous period in the females' lives.

In summary, female preference for large males seems to be due to benefits from reduced harm

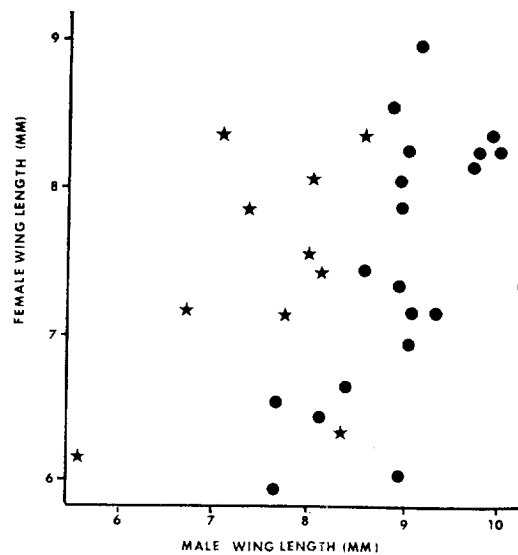


Fig. 4. Ability of paired males to fly at 16 C. Stars indicate those males unable to fly; dots represent those able to fly.

to the female and, possibly, from increased survivorship and growth by offspring. Although it is difficult to determine the relative contributions of protection, escape, and rapid oviposition offered by large males, the consistent advantage they offer to females in proximate benefits during mating suggests that each of these factors may have contributed to the evolution of female mate-preference patterns.

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PLACENTA ON BEHAVIOUR

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Abstract. Previous research (sensitize) more rapidly percentage of virgin rats applied to the skin of the pups and therefore hastened indeed shortened the maturation of the pups, to the presence of placenta. Other attractive significant, shortening of

When maternally naive a behave maternally toward immediately. When maternally housed continuously with (tation), they too behave pups, but not immediately maternal behaviour (latency) to appear is (Wiesner & Sheard 1933; 1966; Rosenblatt 1967). Maternal sensitization latency affected not only by manipulations (see Lamb 1979; Slotnick 1975 for environmental manipulations). Rosenblatt (1971) demonstrated that virgin and pups are forced during concaveation by cages, maternal sensitization shorter. It appears then that sensitization is dependent, at least, on the action of intensity and of the presence of pups. We would expect, therefore, that factors that promote non-maternal behaviour of the female should have a facilitating effect on the latency of maternal behaviour.

Birch (1956) suggested that pups are attracted to pups at the skin of the pups that have their own anogenital areas, and that they are intensely attracted as a result of this. Whether or not this is the case, the pups are reminiscent of anogenital attractants, though they are associated with the skin and are extremely attractive to rats.